COMPARISON OF SNOWSHOE HARE POPULATIONS IN

INTERIOR ALASKA

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A

THESIS

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ABSTRACT

Snowshoe hares, *Lepus americanus*, are a 'keystone' prey species in northern boreal forests and experience population fluctuations of 8-11-years. Despite intense responses of both vegetation and predators to changes in hare densities, landscape-scale comparisons of hare populations in Alaska have been limited to qualitative descriptions. We conducted capture-recapture studies of snowshoe hares at 5 locales in the Tanana valley, from Tok in the east to Clear in the west from 1999 to 2002. Snowshoe hare densities were highest in 1999 ($\bar{x}$=6.36 ha^{-1}, SE=0.63) and declined thereafter. We were unable to detect declines in apparent survival during declining densities in our study populations. Movement distances did not vary temporally and persistence of individuals through declining densities may be associated positively with body condition at the peak. The relationship of hare pellets and hare densities was weak and limits the utility of this methodology for estimating hare densities in Interior Alaska.

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CHAPTER 1

INTRODUCTION

Snowshoe hares, *Lepus americanus*, are a 'keystone' herbivore in northern boreal forests of North America and experience 8-11-year cyclic fluctuations in population abundance (Krebs et al.1986, 2001a, Keith 1990). Fluctuations of hare populations exhibit regularity, high amplitude of 10-25-fold, and temporal transitions from high to low densities of 1 to 3 years (Hodges 2000, Keith 1990). Populations of snowshoe hares in northern boreal forests are primarily influenced by predators and forage, with secondary influences from parasites and disease (Adams 1959, Finerty 1980, Hodges 2000, Krebs et al. 2001a). There is debate as to whether the predators and food species act separately (Stenseth et al. 1997) or in conjunction (Hodges 2000, Hodges et al. 2001, Krebs et al. 2001a) to influence cyclic hare populations.

Snowshoe hare cycles have been described as 4 densities: increase, peak, decline, and low (Keith 1990, Wolff 1980). Population cycles of snowshoe hares have been described on large geographical scales using indirect measures such as the Snowshoe Rabbit Inquiry (Chitty 1950, Smith 1983), analysis of Hudson Bay fur records, (Elton 1924, Moran 1953, Haydon and Greenwood 2000) and Alaska Dept. of Fish and Game (ADFG) trapper questionnaires (Scott and Kephart 2002). The populations of hares react to simultaneous top-down (hare predators) and bottom-up (preferred vegetation) controls (Stenseth et al. 1997). Responses of hares to changing food resources and predation risk include changes in adult and juvenile survival (O'Donoghue 1994, Haydon et al.

1999), reproductive output (Cary and Keith 1979, Ernest 1974, O'Donoghue and Krebs 1992), body condition (Murray 2002), and behavior (Hik 1995).

Predators of hares include lynx (*Lynx canadensis*), coyotes (*Canus latrans*), goshawks (*Accipiter gentilis*), and great horned owls (*Bubo virginianus*) and exhibit 2-10-fold fluctuations in abundance in response to changes in hare abundance (Keith 1990, O'Donoghue et al. 1998). The fluctuations in predator numbers lag 1-3 years behind fluctuations in hare densities (Boutin et al. 1986, Brand et al. 1976, O'Donoghue et al. 1997). The predation hypothesis suggests that the higher mortality rates associated with high predator densities during the hare peak and initial decline are capable of driving the decline in hare densities (Hodges 2000, Hodges et al. 2001, Keith 1990, O'Donoghue et al. 1997). Juvenile survival is especially low during decline densities, thereby limiting number of hares available for breeding the following year (Hodges 2000, O'Donoghue 1994). Furthermore, hare behavior associated with high predator numbers, such as habitat selection for dense cover and increased movement, may lessen body condition of hares, thereby reducing predator avoidance (Boonstra et al. 1998, Hik 1995, Hodges 1999, Murray 2002).

Finerty (1980) concluded that predation was unlikely to be the sole cause of cycles in the abundance of hares and small mammals and argued that food availability was a probable cause of fluctuations of hare densities. High densities of snowshoe hares during peak densities consume available biomass to levels below those necessary to sustain hare populations over winter (Bryant 1987,

Keith 1983, Pease et al. 1979, Sinclair et al. 1988, Smith et al. 1988). The intense browsing by hares further affects vegetation and soil processes by increasing secondary compounds that plants produce, further decreasing quality of the vegetation (Bryant 1987, Fox and Bryant 1984). The intensive browsing of early successional species such as willow (*Salix spp.*), which are relatively preferred by hares, accelerates growth and coverage of later successional species such as alder, which are not preferred by hares (Kielland et al. 1997, Kielland et al. 1998). The densities of vegetative biomass and related habitat cover influence the carrying capacity, predator avoidance, and again, the body condition of hares (Adams 1959, Keith 1966, Wolff 1980, Murray 2002).

In addition to predator and plant control of the hare cycle, parasites and disease may indirectly influence the population cycle of snowshoe hares (Krebs et al. 2001a). High rates of starvation, a possible indication of diseased animals, occur during the decline phase (Boutin et al. 1986, Keith 1990). Snowshoe hares are infected by many nematode and cestode species that have cyclic infestation rates (Cary and Keith 1979, Erickson 1944, Hodges 2000). However, parasite loads have not been linked to lower reproductive output or survival in natural hare populations (Cary and Keith 1979, Bloomer et al. 1995, Murray et al. 1998, Sovell and Holmes 1996).

Interactions of snowshoe hares and plants have been extensively studied in Interior Alaska (Bryant et al. 1985, Bryant 1987, Bryant et al. 1989, Kielland et al. 1997, Ruess et al. 1998). However, there were no concurrent studies on hare

populations as the last were conducted nearly 30 years ago (Ernest 1974, Trapp 1962, Wolff 1980). Research on the population dynamics of snowshoe hares in Interior Alaska occurred near Fairbanks during a peak to decline from 1971 to 1977 (Ernest 1974, Wolff 1980). Wolff (1980) focused upon the effects of habitat quality on local populations of snowshoe hares whereas Ernst (1974) observed population dynamics of hares locally and reproductive output of females regionally. Previously, Trapp (1962) observed the snowshoe hare populations near Fairbanks during an early population increase.

The only landscape-scale description of hare populations in Alaska is that of trapper questionnaires, in which ADFG assesses population trend and abundance for each Game Management Unit (GMU) (Kephart and Scott 2002, see maps at mercury.bio.uaf.edu/~eric_rexstad). Population dynamics of hares in Alaska are known only in qualitative terms, similar to those in the Yukon Territory prior to the Kluane Boreal Forest Project (Krebs et al. 2001b). Snowshoe hare populations are often described qualitatively due to a relatively low economic value leading to lower appropriation of monitoring resources. The population monitoring of snowshoe hare populations on large geographical scales requires indirect measures that combine precision, limited bias and efficiency.

The objectives of this study were to assess temporal and spatial variations in population dynamics of snowshoe hares in Interior Alaska. The study was initiated during high densities of snowshoe hares. Methodological analysis

included quantifying the accuracy of pellet counts as predictors of hare densities in Interior Alaska.

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CHAPTER 1. COMPARISON OF SNOWSHOE HARE POPULATIONS IN INTERIOR ALASKA[1]

Abstract:

Snowshoe hare densities in Interior Alaska from 1999 to 2002 were highest in August 1999 and declined thereafter. Population densities were as high as 8.70 hares ha^{-1} during the peak and less than 0.5 hares ha^{-1} during the low. The low densities continued through March 2002. Movement distances of snowshoe hares varied spatially but not temporally or by sex, contrary to previous studies. Apparent survival of adult hares varied temporally in 2 locales and was constant at 2 other locales. Interior Alaska adult recruitment was highest during high densities and subsequently declined. Adult male body condition did not vary temporally or spatially. However, *a posteriori* comparisons suggested higher body condition during high densities for surviving hares than those assumed to have died.

INTRODUCTION

Ecologists often generalize beyond the limits of spatially explicit data to explain population and ecosystem dynamics (Hodges et al. 2001). Broad spatial inferences based upon locally specific results are suspect when applied to species, such as snowshoe hares, that are broadly distributed across large and

[1] Flora, B.K., E.A. Rexstad, and K. Keilland. Submitted. Journal of Wildlife Management.

heterogeneous landscapes. The findings for such species should be further assessed at multiple spatial scales (Krebs et al. 2001b).

We were interested in the spatial congruence of population dynamics of snowshoe hares in Interior Alaska. Previous snowshoe hare studies in Interior Alaska have not considered large-scale spatial dynamics. The lack of spatial studies precludes assessment of heterogeneity of population dynamics and further increases uncertainty of conclusions concerning population dynamics of hares at landscape-scales (Hodges 2000). Snowshoe hares have a wide distribution and occupy a variety of climates and habitats (Murray 2000). Conceivably, if climate and habitat drive population dynamics of hares, we might see differences in the dynamics of populations experiencing different influences. The simultaneous comparison of population dynamics of hares at a broad scale in Alaska may differentiate temporal and spatial variation among the studied populations.

Snowshoe hare populations in boreal forests are the primary prey source for boreal predators and exhibit regular 8-10-year fluctuations in population which are hypothesized to be spatially and temporally synchronized (Hodges 2000, Hodges et al. 2001, Krebs et al. 2001a). Hare populations are influenced by a 3-trophic interaction of snowshoe hares, predators and browse availability (Hodges 2000, Hodges et al. 2001, Keith 1990, Krebs et al. 2001a, Murray 1998, O'Donoghue 1997) with modifying influences such as parasites and disease (Hodges et al. 2001, Krebs et al. 2001a, Murray et al. 1998). Though body

condition of hares diminished during a decline in the southern part of their geographical range due to food shortage (Hodges et al. 1999b, Keith et al. 1984, Murray 2002, O'Donoghue and Krebs 1992, Vaughan and Keith 1981), physically substandard hares were not disproportionately vulnerable to predation (Murray 2002, Wirsing et al. 2002). Therefore, the hypothesis that lower body condition of hares leads to starvation, increased predation (Wolff 1979, Murray 1999, Hodges 2000) and decreased reproductive output remains inconclusive (Boonstra et al. 1998, Hodges et al. 1999b). However, the lowest body conditions and survival occur during the decline rather than the low or peak densities (Hodges et al. 2001, Murray 2000). Hares that survive the decline occupy habitat refugia, and populations begin increasing when browse has recovered and predator numbers have diminished (Wolff 1980).

Boonstra et al. (1998) surmised that predation risk, and not high hare density or poor nutritional condition, accounted for lower body condition and reproduction characteristic of the decline because food availability remained high. Low densities of hares may be prolonged due to behavior associated with escaping and avoiding predators increasing energy expenditure, thereby decreasing fitness of the hares (Hik 1995).

Snowshoe hares influence vertebrate and plant populations in northern boreal forests (Krebs et al. 2001a). For instance, predator densities change 2-10- fold concurrently with similar changes in snowshoe hare abundance (Boutin 1995, Hodges 2000, Keith 1990, O'Donoghue et al. 1997). Additionally, small

herbivore populations may become the alternative prey of hare predators during the low (Boutin et al. 1995). Microtine (*Microtus spp.*) populations in the Yukon Territory, Canada peaked 3 years after a peak in densities of snowshoe hares because of soil nutrient input from hare pellets deposited at peak densities of hares (Boonstra et al. 2001). Third, browsing by snowshoe hares affects vegetation and soil processes (Bryant 1987, Bryant et al. 1989, Kielland et al. 1997). Winter browsing by snowshoe hares reduced the production of fine roots and decreased fine root longevity, accelerated carbon turnover, thereby accelerated succession from willow to alder (Kielland et al. 1997, Kielland et al. 1998, Ruess et al. 1998).

Snowshoe hare populations were studied near Fairbanks, Alaska from 1971 through 1977 and included the peak, decline, low, and early increase densities of a population cycle (Ernest 1974, Wolff 1980). Snowshoe hare populations in Interior Alaska have peaked in 1961, 1971, and 1988-89, and lows occurred in 1955, 1965, 1975, and 1993-94 (Ernest 1974, Hodges 2000, Trapp 1962, Bonanza Creek Site Long-Term Ecological Research, unpublished data, Wolff 1980). However, spatial comparisons of population dynamics of Alaska hares has not occurred with the exception of a comparison of female reproduction by Ernest (1974).

Research on population dynamics of snowshoe hares in Alaska provides herbivore data for comparisons with concurrent or previously collected furbearer and vegetation data. The objective of our study was to describe the population

dynamics of snowshoe hares in Interior Alaska spatially and temporally from March 1999 to March 2002. Our investigation of population dynamics of snowshoe hares included estimates of densities, survival, and recruitment, and indices of movement distances and body condition.

STUDY AREA

Our 4 study sites were along the Tanana River in Interior Alaska (Fig. 1.1). There were 2 grids at the Bonanza Experimental Research Forest 20 km south of Fairbanks (Bonanza Riparian: N64°41'36.6", W148°17'30.3 and Bonanza Mature: N64°41'41.7, W148°17'03.4"), and 1 site each at Clear Air Force Base (Clear: N64°17'23", W149°06'57.1"), Mile1408 on the Alaska Highway (Delta: N63°54'50.2", W145°21'43.5"), and Mile 97 of the Tok Cut-off Highway (Tok: N63°01'54.8", W143°22'14.5") (Fig. 1.1). The 4 sites contain independent snowshoe hare populations because the closest distance between adjacent study sites was approximately 80 km. The longest dispersal of a hare documented was a juvenile female that traveled 20 km, well under the distances between our sites (O'Farrell 1965).

The sites were early to mid-successional forests that had been disturbed by fire or floods 15 to 40 years ago. Bonanza Riparian is a flood zone along the Tanana River and Bonanza Mature is a mature black spruce forest approximately 1 km inland from the river and 2 km from the riparian plot. Bonanza Riparian consisted of willow (*Salix spp.*), paper birch (*Betula papyrifera*), alder (*Alnus*

spp.), white spruce (*Picea glauca*), fireweed (*Epilobium augustifolium*) and several grasses. Bonanza Mature consisted of stands of mature white spruce, paper birch, and alder, as well as black spruce (Picea *mariana*), Labrador tea (*Ledum groenlandicum*), willows, and prickly rose (*Rosa acicularis*). Clear was located in a mid-successional forest mostly comprised of aspen (*Populus tremuloides*), birch, and white spruce with areas of black spruce and Labrador tea. Delta consisted of birch and aspen stands intermixed with open areas of downed spruce and lower canopy growth such as fireweed and prickly rose. Tok was comprised of black spruce stands and Labrador tea as well as patches of alder and willow.

The coldest month in Interior Alaska (January) averages -24.9°C with minimum temperatures near –50°C, whereas the summer temperatures may rise near 35°C, with the warmest month of the year (July) averaging 16°C (Bonanza Creek Site Long Term Ecological Research, unpublished data). Precipitation in Interior Alaska averages 26.9 cm annually, and annual snowfall averages 140 cm per year (Fairbanks) with snow cover typically persisting from October to late April (Bonanza Creek Site Long Term Ecological Research, unpublished data, Viereck and Little 2000).

METHODS

Live trapping

Snowshoe hare populations were monitored at the 5 trap grids from March 1999 to March 2002. The trap grids were approximately 9 hectares and consisted of 7 transects with 7 traps each and 50 m inter-trap distance. This is because hare home ranges typically are 5 to 10 ha, and overlap is common (Hodges 1999, Hodges 2000, Wolff 1980). Bonanza Riparian consisted of 10 transects with 5 traps each because river erosion encroached on the narrow band of riparian habitat along the river. Wolff (1980) used 80 traps in an 8*10 array with 60 m separating each trap, and Hodges et al. (2001) employed 86 traps per site on 4 transects spaced 150 m apart and the inter-trap distances along transects was anywhere from 30 to 60 m. The traps at Bonanza were Havahart size 3 and the traps at the other sites were designed according to Cushwa and Burnham (1974). We modified the Cushwa and Burnham (1974) design by lengthening the floor platform to 16 cm to prevent hares from stepping over the trigger and thereby avoiding capture.

Using the terminology of Nichols and Pollock (1990), each population was monitored in 4 primary encounter occasions per year (June, August, November, and March) to correspond with the life history stages of hares. This allowed for intra-annual and inter annual comparisons among the 5 trap grids. Primary encounter occasions occurred over the course of 5 weeks and consisted of 8-10 secondary encounter occasions (individual examinations of trap grids). Similar to

other studies of snowshoe hares, the traps were baited with carrots for hydration and alfalfa for nourishment (Hodges et al. 2001, O'Donoghue and Krebs 1992, O'Donoghue et al. 1997, Wolff 1980). Summer traps were set during the evening and checked twice per day for 5 subsequent days. Winter traps were set in the evening and examined for 4 subsequent mornings and closed during the day to prevent mortalities. Trap sickness, a condition caused by overexposure to hot, cold, or wet conditions, causes weakening that leads to coma and eventually fatal convulsions (Keith et al. 1968). We employed the Keith et al. (1968) technique of injecting 1-3cc of 50 percent dextrose solution when hares displayed trap sickness (UAF IACUC protocol #99-14).

Each snowshoe hare captured was sexed, weighed (±5g), and the right hind foot was measured (mm), and newly captured hares were tagged with No. 3 Monel tags from the National Band Company (Boonstra et al. 1998, Hodges et al. 1999a, Hodges et al. 2001). Adult males were defined as those with a pointed penis while juveniles were those with a smaller, blunt and barely eversible penis (Keith et al. 1968, Keith 1990). Females were described as adult when lactating or carrying a fetus according to criteria of Keith et al. (1968) and O'Farrell (1968). When other methods were not applicable, those hares that weighed less than 1100 g or with foot sizes less than 130 mm in June, August, or November were categorized as juveniles, and juveniles became adults the March following their summer of birth.

Data analysis

Density estimation

Population estimates were made using closed model type in Program MARK (White et al. 1999). The objective in developing various models and their associated estimators in Program MARK is to allow the selection of the best estimator for any given set of capture-recapture data, using temporal, behavioral, and heterogeneous parameterization of capture probability (Otis et al. 1978, White et al. 1982) (Table 1.1). Primary encounter occasions were transformed into capture histories specifying the secondary encounter occasion in which the individual was captured (Otis et al. 1978, White et al. 1982). The primary encounter occasions were then stratified according to whether there were recaptures of individuals. If there were no recaptures within a primary encounter occasion, then abundance was equated to number of hares caught. Otherwise, models were fit to secondary encounter occasions so that a wide array of models could be fit to data-rich trapping occasions. Models incorporated capture probabilities that varied temporally, in behavioral response, individual heterogeneity, and combinations of the 3 (Otis et al. 1978) (Table 1.1). Closure was assumed during each of the primary encounter occasions, as methods to test for closure currently assume either only temporal (Stanley and Burnham 1998) or heterogeneous (Otis et al. 1978) variation.

Estimates from models that contained estimable parameters, such as those where recaptures of individuals occurred, were model-averaged, allowing

inferences to be based on more than a single model (Buckland et al. 1997). By averaging estimates over all models, model selection uncertainties were included in the estimate of precision of parameters and unconditional estimates of variances and standard errors were produced (White et al. 1999). The abundances of primary occasions were estimated for each site from the sum of male and female abundances. In the case of inadequate recaptures of either sex, the abundances were fit to models without sex-specific parameters.

Snowshoe hares may modify their home range size in response to breeding, food supply, population density and predators (Hodges 2000), thereby causing variation in effective trapping area. Effective trapping area was calculated from the mean maximum distance moved (MMDM) and the associated error using the equation $(L+MMDM*d)^2$ (where L= length of 1 side of grid, d is the inter-trap distance) (Wilson and Anderson 1985). MMDM is the average maximum distance (straight line) animals moved between captures within a primary trapping session (Wilson and Anderson 1985, Wolff et al. 1997). Abundance estimates of the trap grids were divided by effective trapping area to compute density. Spatial and seasonal variation in movements (MMDM) of hares were examined by applying a 6-way analysis of variance (ANOVA) (PROC GLM, v.8.2; SAS Institute 2001) using location, month, year, season (summer or winter), sex, and age effects. Significance of main effects and interactions were analyzed using type III sum of squares.

Apparent survival estimation and recruitment

We used Pollock's robust design in Program MARK to estimate apparent adult survival (White and Burnham 1999). Collecting capture-recapture data under Pollock's robust design provides an additional source of information on capture probability that can be exploited statistically to provide less biased and more efficient estimates of survival (Kendall 1999). Models of robust design in MARK have 6 sets of parameters denoted as: apparent survival (Φ), temporary emigration (γ') temporary immigration (γ''), capture probability (p), recapture probability (c), and abundance (N). Our capture histories of individuals were designed according to Lebreton et al. (1992) and included all adult encounters from June 1999 to March 2002. The intervals between primary occasions were transformed to produce the 30-day apparent survival described in other snowshoe hare studies (Hodges et al. 2001, O'Donoghue and Krebs 1992, Gillis 1999). Apparent survival was assessed jointly at Bonanza sites and at Clear and Delta sites due to an additional secondary encounter occasion in November 2001 at Bonanza. Apparent survival in Tok was analyzed separately because too few individuals were captured following June 2000. Temporary emigration and immigration parameters were fixed at 0 throughout the analysis to concentrate analysis upon parameters of apparent survival that were biologically relevant. Furthermore, abundances for primary encounter occasions were fixed at number of adult hares captured if there were no recaptures and denoted as M_{t+1} similar to Otis et al. 1978).

A parameter-rich model was attempted first and subsequent models were constrained in a step-down approach (Lebreton et al. 1992). Biologically plausible sources of variation, such as temporal and behavioral, were used in building the models. Initially, models were fit to capture and recapture parameters. The survival parameters retained location and time effects because survival was of greatest biological interest (Lebreton et al. 1992). Capture and recapture probabilities included similar variation as those models in closed model abundance estimation (Table 1.2), in addition to summer and winter variation (season), month of primary occasion variation (m), and annual variation (y). Model averaging, explained in density estimation methods above, was applied. The most parsimonious capture-recapture model structure from Akaike Information Criterion (AICc) (Akaike 1973) comparisons was then maintained in subsequent survival modeling for investigation of biologically relevant variation such as location, year, season and month.

Adult population recruitment among primary trapping occasions was assessed using Jolly-Seber recruitment and the variance derived applying the Delta method (Pollock et al. 1990: 20). The equation is a function of population abundance and survival from i to i+1, where i is time and B_i is recruitment:

$$B_i = \hat{N}_{i+1} + \hat{\phi}_{i+1}(\hat{N}_i)$$ (Pollock et al. 1990: 20).

The Pollock et al. (1990) recruitment estimate is similar to the population dilution rate (Krebs 1989) applied in Hodges et al. (2001a).

Body Condition

A body condition index has often been used to describe physiological changes of snowshoe hares during fluctuating densities (Hodges et al. 1999b and O'Donoghue and Krebs 1992). Snowshoe hare body conditions were estimated by dividing mass (g) by right rear foot length (mm) similar to that described in Bailey (1968). Mass and foot length were based on measurements of mass for the first captures for each animal in the corresponding primary encounter occasion. This is because animals captured multiple times in a session may experience weight loss and cause bias in estimates (Bailey 1968). Adult male body condition was described for all seasons, but female body condition was assessed only during winter, because most females are pregnant during summer and mass is influenced by gestation stage (O'Donoghue and Krebs 1992). Juvenile body condition was excluded due to our inability to differentiate between litters. We assessed the response of body condition of adult male hares to month, year, season, and location effects using a 4-way ANOVA and adult female hares to location, month, and year using a 3-way ANOVA (PROC GLM, v8.2; SAS Institute 2001). To further test changes in body condition of snowshoe hares with changing hare densities, we assessed the response of body condition of hares from the 1999 cohort to persistence (survival past June 2000) and location using a 2-way ANOVA. Significance of ANOVAs was tested using type III sum of squares.

RESULTS

Density estimation and movement

The populations of snowshoe hares in Interior Alaska attained their highest densities, adjusted for movement (MMDM), approximately in August 1999 and declined thereafter (Fig. 1.2). Over the course of 332 secondary encounter occasions (8 primary encounter occasions), 552 animals were captured, of which included 97 hares in Clear, 109 hares in Bonanza Mature, 191 hares in Bonanza Riparian, 71 hares in Delta, and 84 hares in Tok. The highest densities of snowshoe hares were 8.77 ha^{-1} (SE=1.87) in Tok and 7.38 ha^{-1} (SE=1.47) at Bonanza Mature during August 1999 (Fig. 1.2). Densities remained low until March 2002, the end of our study (Fig. 1.2).

Estimates of MMDM included 170 snowshoe hares (105 males and 65 females) captured in at least 3 secondary encounter occasions of the corresponding primary encounter occasions. An ANOVA using Type III sum of squares showed that location was a significant variable influencing MMDM ($F=2.68$, $df=4$, $P=0.037$) along with the interactions of location and year ($F=2.26$, $df=7$, $P=0.035$) and month and year ($F=4.75$, $df=2$, $P=0.01$). The remaining factors and interactions had no significant effect on snowshoe hare movement ($P>0.05$). Effective grid size is a function of movement; therefore, the movement ANOVA corresponds to comparisons of effective grid size. Effective grid size predominately varied spatially with limited temporal variation from March 1999 to March 2002 (Fig. 1.3).

Density estimation techniques

Density estimation of primary encounter occasions was dependent upon both the number of hares captured and movement (MMDM) of recaptured individuals. Primary encounter occasions with no recaptures resulted in abundance estimates that were the number of hares captured rather than estimates based on probabilities of capture and recapture. Grid area estimated from hare movement became the only source of variation if movement was estimable and abundance was inestimable. Approximately 90% of uncertainty in density estimates during high densities (August 1999) was due to abundance estimates because the high number of recaptures during this primary occasion produced more precise estimates of MMDM. However, abundance estimates influenced uncertainty of density estimates nearer 60-70% during the low population densities of June 1999 and 2000. The decrease in influence of abundance estimates on uncertainty may have been from MMDM estimation having higher uncertainty. The increased uncertainty of MMDM may stem from fewer individuals incorporated into the estimate.

Population densities and their associated variances were estimated from the sum of male and female abundance from June 1999 to November 2000 (Table 1.1). Site abundances were derived without sex variation in capture-recapture parameters at Bonanza Riparian in March 1999 and at Clear, Delta and Tok in June 1999 (Table 1.1). The most preferred models employed in abundance estimation when sexes were summed did not include variation in

capture and recapture probabilities (Table 1.2). All 5 trap grids were assessed concurrently during August 1999 and 2000 with preferred models being p(t*h)=c(t*h) and p(d*s)=c(d*s), respectively (Table 1.2, refer to Table 1.2 caption for description of model notation). Probabilities of capture-recapture varied for those 3 model groups whose abundance estimates were derived without incorporating sex variation into model selection (Table 1.2). Uncertainty in types of variation in capture-recapture probabilities accounted for 0 to 30% of the uncertainty in density estimates in data sets where abundance was estimable (not equaling M_{t+1}).

Apparent survival and recruitment

Apparent survival was estimated using robust design in Program MARK with temporary emigration and immigration assumed to be 0. The population parameters that were non-estimable in abundance analysis using closed model type, primary encounters with no recaptures, were fixed at M_{t+1}. At the Bonanza site, model selection of capture-recapture probabilities of snowshoe hares based upon AICc identified seasonal variation in both primary encounter occasions (summer and winter) and diurnal variation of secondary encounter occasions (morning and evening encounters) (Table 1.3). At Clear and Delta, model selection of capture-recapture probabilities based upon AICc identified variation among primary encounter occasions (June, August, November and March) and diurnal variation of secondary encounter occasions (Table 1.3). At the Tok trap grid, model selection of capture-recapture probabilities, based on AICc, identified

diurnal variation of secondary encounter occasions (Table 1.3). Probability of capture-recapture for winter encounters was 2.5 times that found for summer encounters at Bonanza; whereas, probability of capture was similar among morning encounters during winter and summer at Clear and Delta. In summer, probability of capture during morning encounters was typically 3-5 times higher than that for evening encounters for all sites.

The most parsimonious models of capture-recapture were applied in the analysis of apparent survival. Location was the highest source of variation (AICc weight = 0.60) in apparent survival at Bonanza with temporal variation having a lesser effect (Table 1.4a). The interaction of location and time for capture-recapture probabilities among primary encounter occasions affected apparent survival in Clear and Delta (AICc weight = 1.0, Table 1.4b). Apparent survival in Tok (June 1999 to August 2000) varied slightly as the model in which survival did not vary temporally, $\Phi(.)$, had the highest AICc weight (0.47), and there were small effects resulting from seasonal (AICc weight = 0.27) and temporal (AICc weight = 0.26) variation (Table 1.3c).

Apparent survival (30-day) among primary encounters remained constant in Bonanza Mature and Riparian, whereas, apparent survival declined in Clear and Tok during the summer of 2000, coinciding with the initial decline in hare densities (Fig. 1.4). The highest apparent survival (30-day) occurred in Delta (0.93, SE=0.02) and Clear (0.92, SE=0.03) from August 1999 to June 2000 (Fig. 1.4). Estimates of apparent survival (30-day) for Clear, Delta, and Tok ranged

from 0.63 (SE=0.14) to 0.68 (SE=0.24) during the corresponding low hare densities (Fig. 1.4). Apparent survival uncertainty attributable to model selection ranged from 22-37% and 2-10% for Bonanza Mature and Bonanza Riparian, respectively. The data-rich model for apparent survival for Clear and Delta that included both temporal and location variation did not have competing models because the AICc weight was 1.0 on a scale of 0 to 1 (Table 1.4b). Apparent survival uncertainty attributable to model selection varied from 7 to 69% in Tok.

Application of recruitment estimation described in Pollock et al. (1990:20-21) showed adult recruitment to be highest from August 1999 to June 2000 at all sites except Clear (Fig. 1.5). Adult recruitment was highest in Clear, the most western of the trap grids, from August 2000 to November 2000 (Table 1.5). Adult recruitment was less than 10 hares per 9 ha in Tok during all intervals after June 2000 (Fig. 1.5). Recalculation of adult recruitment from hare densities (Fig. 1.2) and adult survival (Fig. 1.4) would be erroneous, as we estimated recruitment using abundance of only adult hares rather than abundance of all animals captured. Estimates of adult recruitment should be viewed as indices rather than as absolutes, as abundances incorporated into Pollock et al. (1990) were not adjusted for MMDM because too few adults were recaptured. Abundances not corrected for movement tend to be higher than those corrected for movement, possibly influencing recruitment estimates. The number of adult hares recaptured during primary encounters subsequent to the high densities in August 1999 was inadequate for precise and unbiased estimates of MMDM.

Furthermore, temporal intervals among primary occasions were not constant, with the longest interval being August 1999 to June 2000 (8 months). However, the intervals from June 2001 to March 2002 were all approximately of the same duration and described recruitment as decreasing with declining hare densities (Fig. 1.5).

Body Condition

The ANOVA model assessing body condition of male hares suggested no temporal or spatial changes in body condition with declining hare densities among month, year, season, or location effects ($P>0.1$, Fig. 1.6). There were qualitative differences among body condition associated with survival of male hares past peak densities for persistence and location effects; however, the differences were not significant in ANOVA ($p>0.05$) (Fig. 1.7). Of the hares from the August 1999 cohort, those that persisted through declining densities qualitatively had better body condition than those hares assumed to have died at Clear, Bonanza Mature, and Bonanza Riparian (Fig. 1.7). Only One hare from the August 1999 cohort in Tok persisted past peak densities (Fig. 1.7). The ANOVA assessing body condition of adult females in winter showed no influencing factors or interaction effects ($P>0.1$).

DISCUSSION

Snowshoe hare density

We described the population dynamics of snowshoe hares in Interior Alaska at a regional spatial scale from March 1999 to March 2002. Populations of snowshoe hares in Interior Alaska most recently peaked in August 1999 and the decline began during the winter of 1999-2000. The densities of hares in Interior Alaska during the spring prior to the 1999 peak ranged from 0.8 to 2 hares ha^{-1}, comparable to that found during the peak in 1989-90 in the Yukon Territory, Canada (Hodges et al. 2001). Meanwhile, the peak densities in our study ranged from 3.35 to 8.70 hares ha^{-1}. The density of 7.38 hares ha^{-1} at the Bonanza Riparian trap grid was approximately 9.6 kg ha^{-1} of hare biomass, more than fifteen times the estimated 0.59 kg ha^{-1} of hare biomass estimated during the decline (August 2001) at Bonanza Riparian (0.45 hares ha^{-1}). Meanwhile, moose biomass during early fall on the Tanana River flats was approximately 4.4 kg ha^{-1} during the course of our study, using a density of 1.1 moose km^{-2} (Seaton 2002) and a mean mass of 400 kg per moose (Seaton pers. comm., Alaska Department of Fish and Game). This qualitative assessment of relative magnitude of biomass during the course of the study illustrates hares influence on the boreal community in terms of mass of vegetation they consumed and availability biomass for predators.

Historical snowshoe hare populations studied in Alaska were re-analyzed by Keith (1990) incorporating current estimation methodology and were 6 hares

ha^{-1} during the 1971 peak, 1.5 to 2.2 hares ha^{-1} the first 2 years post-peak from 1972-3, and 0.2 hares ha^{-1} during the low in 1975 (Ernest 1974, Wolff 1980). Snowshoe hare densities were approximately 3.8 hares ha^{-1} during peak densities in 1961 (Trapp 1965). Peak densities in our study (August 1999) suggested higher hare densities than the peaks studied in 1961 and 1971. Hare densities in our study were higher in August than June for all 3 years and mostly a function of juvenile recruitment during the summer. The transition from peak to low densities typically occurs in 1 to 3 years (Hodges 2000). In our study, the transition from high densities to those where we had too few captures to produce abundance estimates was approximately 2 years, similar to the transition from peak to low densities described by Ernest (1974) and Wolff (1980).

The Alaska Dept. of Fish and Game (ADFG) described the fluctuations in abundance of the most recent population cycle initiating in the east and progressing west among ADFG Game Management Units (GMUs) (Kephart and Scott 2002, see maps at mercury.bio.uaf.edu/~eric_rexstad). The public was asked to identify hare populations as abundant, common, or scarce for each game management unit (GMU). Hare populations in Alaska were mostly scarce in 1992-1993 for most of the state and the increase began in the eastern interior of Alaska. By 1998 and into 2000 hares were described as abundant in most GMUs, which corresponded with the highest densities of our study in August 1999. The hare populations were described as common in most GMUs in 2001-2002, with populations in the GMUs near Canada being classified as scarce.

Despite the subjective synchrony of abundances described by the ADFG trapper questionnaires, the quantitative assessment of spatial synchrony was not possible in our study because of uncertainty associated with our density estimates. Ranta et al. (1997) and Bounaccorsi et al. (2000) have described methods to assess spatial and temporal synchrony of populations; however, their methods do not incorporate error of density estimates. Therefore, synchrony analysis of populations must await improved quantitative methods.

Density estimation techniques

We employed Program MARK to estimate abundances of snowshoe hares in Interior Alaska incorporating variation in probabilities of capture and recapture. Program MARK allows the selection of the best estimator for any given set of capture-recapture data using temporal, behavioral, and heterogeneous capture probabilities (White et al. 1982). Furthermore, we were able to employ a larger array of models than typical of snowshoe hare research, including additional sources of variation such as that between morning and evening encounter occasions, sexes, and among locations.

Naïve density estimates are those which apply a trapping area not adjusted for animal movement. Adjustment of naïve density estimates by effective sampling area decreases the overestimation of true densities (Wilson and Anderson 1985). Our naïve trapping area was similar to the 5 to 10 ha home range typical of snowshoe hares (Hodges 2000, Wolff 1980). Uncertainty of our density estimates may have been less had we employed larger trap grids

because edge effect is lessened if trap grids are large relative to size of home range (White et al. 1982:120). However, 9 ha trap grids are justifiable because snowshoe hares often occupy subsets of their home range and individual home ranges often overlap (Hodges 1999). Furthermore, the reliability of MMDM estimates may vary between high and low densities. The estimation of edge effect requires a sufficient number of recaptures to provide reliable estimates of MMDM (Wilson and Anderson 1985). In our study, the uncertainty of effective grid size was lowest during the hare densities at the peak because there were more recaptures. Therefore, the incorporation of the MMDM adjustment of densities relies upon whether MMDM estimates are as accurate during the low, when few individuals are encountered, as those at the peak.

Survival

Apparent survival of snowshoe hares from 1999 to 2002 varied temporally at only 2 of the 5 trap grids. Additionally, apparent survival differed by trap grid between Clear and Delta and between Bonanza Mature and riparian, respectively. Apparent survival was estimable in Tok only from June 1999 to August 2001, and there was only slight variation in seasonal (summer and winter) and temporal effects. Apparent survival during the summer (2000) following high densities was much less than that (1999) during high densities; however, there was high uncertainty in the estimates that prevented quantitatively based conclusions.

Survival has been described as lower during the decline than during the peak (Hodges 2000, Krebs et al. 1986). Mean apparent survival among the trap grids was 0.87 (SE=0.09) during approximate peak densities and 0.81 (SE=0.11) during declining densities. However, the difference in peak to decline apparent survival is only qualitative due to the corresponding uncertainty of the estimates. Similar to our estimates of apparent survival from 1999 to 2002, the 30-day survival for declining densities in 1971 in Interior Alaska ranged from 0.84 to 0.87 (Wolff 1980).

Spatial population changes

Population recruitment of adult hares in Interior Alaska was highest during the 1999 peak and declined thereafter. Recent research in the Yukon Territory revealed juvenile recruitment to be higher during the peak in 1989-90 than for the 1991-92 decline and highest during the 1994 low (Hodges et al. 1999a). Recruitment of hares in Interior Alaska differed from that estimated in the Yukon Territory (Hodges et al. 2001) in that Interior Alaska recruitment continued to decrease into the low phase. Recruitment estimates from the Yukon Territory did not include uncertainty (Hodges et al. 2001). In our study, recruitment estimates did not incorporate movement adjustments in estimates of adult abundance. Therefore, estimates of recruitment in our study and most literature (Hodges 2000, Hodges et al. 2001, Keith 1990) should be viewed as illustrative rather than as absolute.

A hypothesis that deserves further attention is whether the decline in densities of snowshoe hares results from hares of lower body condition during peak densities dying. The decline may then be accelerated by lower recruitment of juveniles to adulthood resulting from high predation. The hares originating from the peak densities in 1999 that persisted on the trap grids qualitatively averaged better body condition than those that were assumed dead at three of the trap grids. Krebs et al. (2001a) described food quantity and quality as affecting body condition and may predispose hares to predation, increased parasite loads, and increased levels of chronic stress. These effects, combined with the decline in recruitment, may support the hypothesis that lower forage availability and increased predation risk during declining densities may cause decreasing body condition that subsequently reduces recruitment (Hodges 2000, Hodges et al. 2001). Snowshoe hares differing in body condition did not respond to predation effects in the southern portion of hare range (Murray 2002, Wirsing et al. 2002); however, the predation risk of hares differing physiologically deserves further attention in the northern range of snowshoe hares.

Possible heterogeneity in the population dynamics of predators and distributions of forage among the trap grids may have influenced population dynamics of the snowshoe hares observed here. For instance, movements of snowshoe hares have been found to increase in response to high predation risk and low forage availability (Hodges 1999, Hodges 2000). The spatial variation of movements among the 5 trap grids and response of body condition of hares to

persistence may provide further evidence that population dynamics of snowshoe hares are spatially and habitat specific.

Spatial extrapolation among locations

Spatial extrapolation among the trap grids in our study did not support spatial uniformity of population dynamics of hares in Alaska. If we had applied the hare densities in August 1999 at Tok, Delta and Clear and their respective apparent survival from 1999 to 2002, then our assessment of hare populations at Bonanza would have been inaccurate. Peak densities in August 1999 qualitatively described peak densities as progressing from east to west. Apparent survival of Clear and Delta varied temporally. Because Bonanza is located between Delta (5.76 hares ha^{-1}) and Clear (3.38 hares ha^{-1}), we may have projected that densities in the Bonanza trap grids would be 4 to 5 hares ha^{-1} in August 1999 and the apparent survival at Bonanza from 1999 to 2002 would vary temporally. Because population densities at Bonanza Mature and Bonanza Riparian were 7.38 hares ha^{-1} and 6.60 hares ha^{-1}, respectively, and apparent survival did not vary temporally, spatial uniformity among the 5 trap grids studied was not illustrated.

MANAGEMENT IMPLICATIONS

Snowshoe hares have been described as 'keystone species' in the northern boreal forest (Krebs et al. 2001a). This is because populations of snowshoe hares have a large impact on plant dynamics and are a primary prey

source for many vertebrates in the boreal community (Bryant 1987, Keith 1990, Hodges 2000, Hodges et al. 2001, Krebs et al. 2001). Hodges et al. (2001) were successful when they described many complex factors that influence the interactive ecosystem dynamics in the boreal forest of the Yukon Territory. However, conclusions may be flawed if wildlife biologists and forest ecologists applied the results from the Kluane Project in areas that simply shared similar biotic and abiotic factors prior to testing the actual similarities of the populations and ecosystems. Future research of snowshoe hares should find significant relationships for estimating regional population dynamics from local-scale investigations.

Population densities of hares in Interior Alaska from 1999 to 2002 were similar to previous hare research in Alaska and Yukon Territory in that populations declined for 2 years following the approximate peak. However, comparisons among studies are difficult because a multitude of mark-recapture estimation techniques have been applied in snowshoe hare research, absence of specified error in much of the historical data, and differences in trap grid sizes and designs (Hodges 2000, Keith 1990). Therefore, standardization of trapping and estimation methodology should be a consideration for future spatial comparisons of small mammal populations that are cyclic.

The snowshoe hare cycle has been studied in the boreal forest of North America for 70 years and much of the phenomenon has been described (Hodges 2000, Keith 1990, Krebs et al. 2001a). However, quantitative assessment of

population dynamics of snowshoe hares spatially remains relatively unstudied (Keith 1990, Hodges 2000, Krebs et al. 2001a). Finding the scale at which local conclusions can be extrapolated to a landscape with accuracy would increase efficiency in estimating hare populations. Lastly, broadening the scope of spatial and temporal comparisons specific to snowshoe hares to those of snowshoe hare predators, competitors, and food resources would further our understanding of the impact of snowshoe hares in northern boreal forests.

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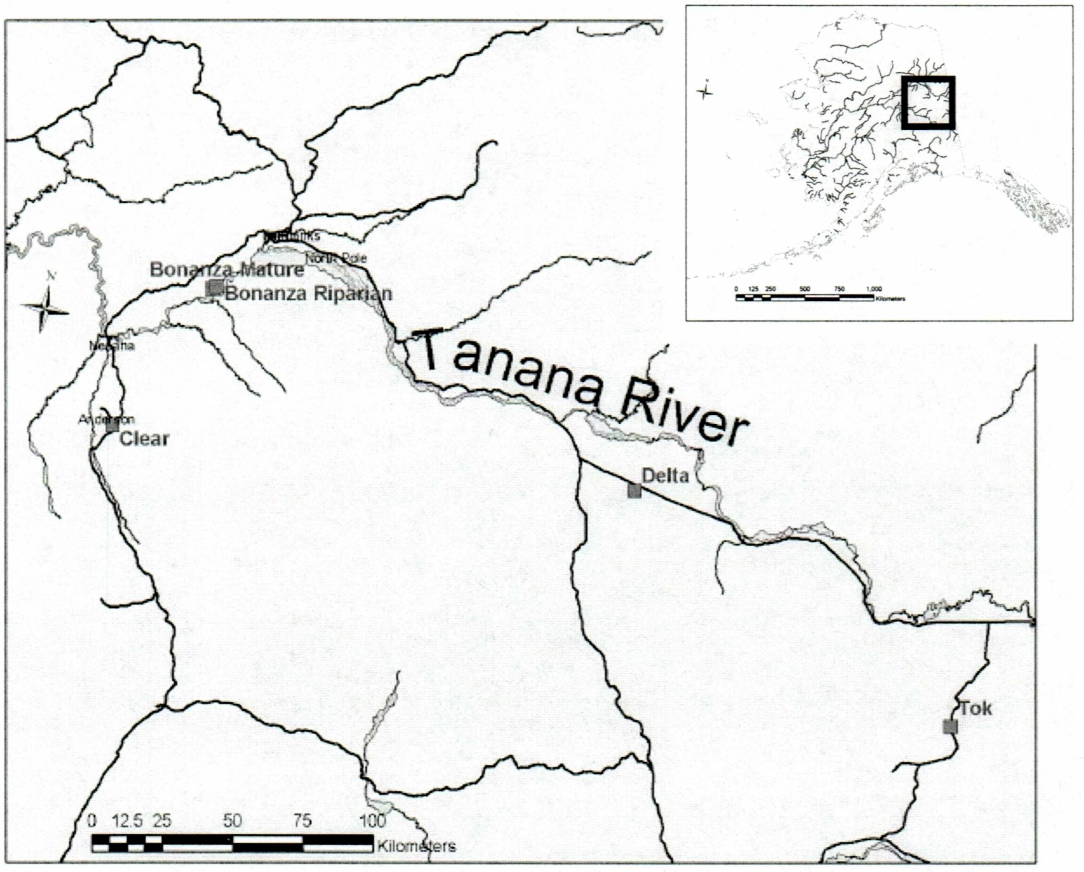

Figure 1.1. Locations of trapping grids (■) along the Tanana River, Alaska, USA.

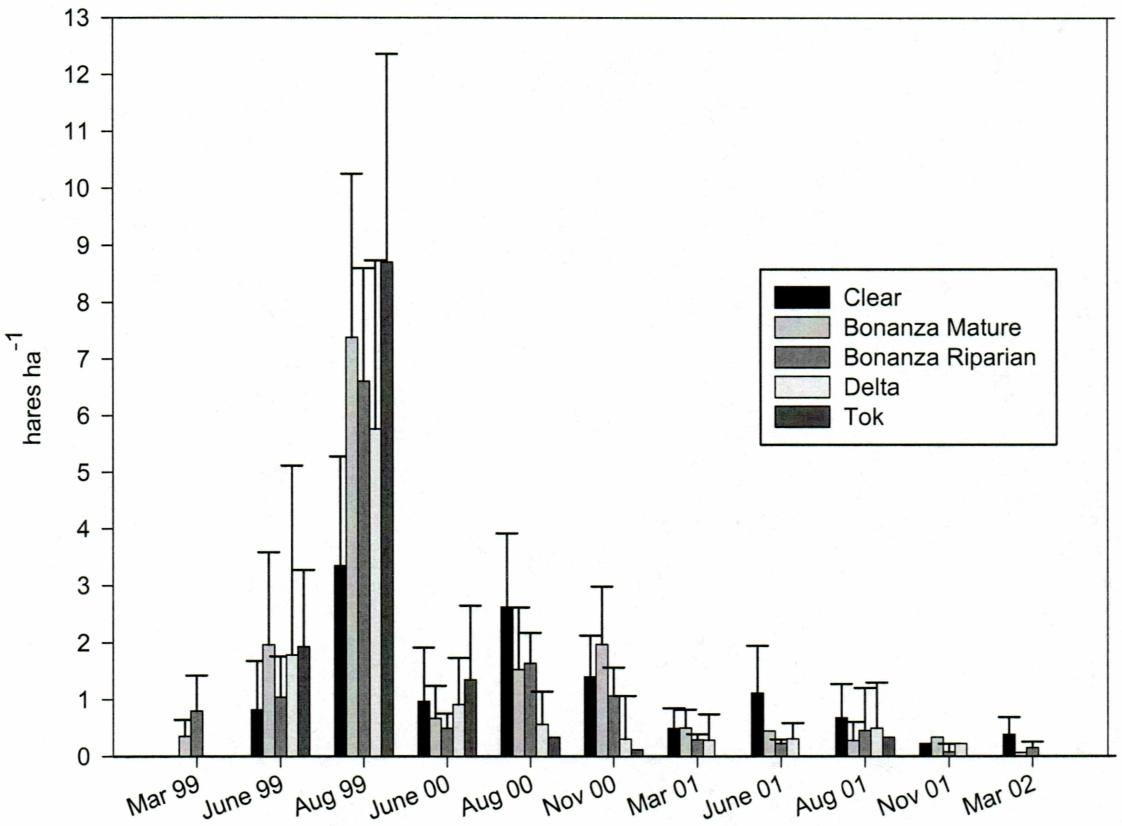

Figure 1.2. Snowshoe hare density estimates, adjusted for movement, at 5 trapping grids in Interior Alaska from March 1999 to March 2002. Error bars represent 95% confidence intervals and primary encounter occasions from March 1999 to March 2002, approximately 4 times per year.

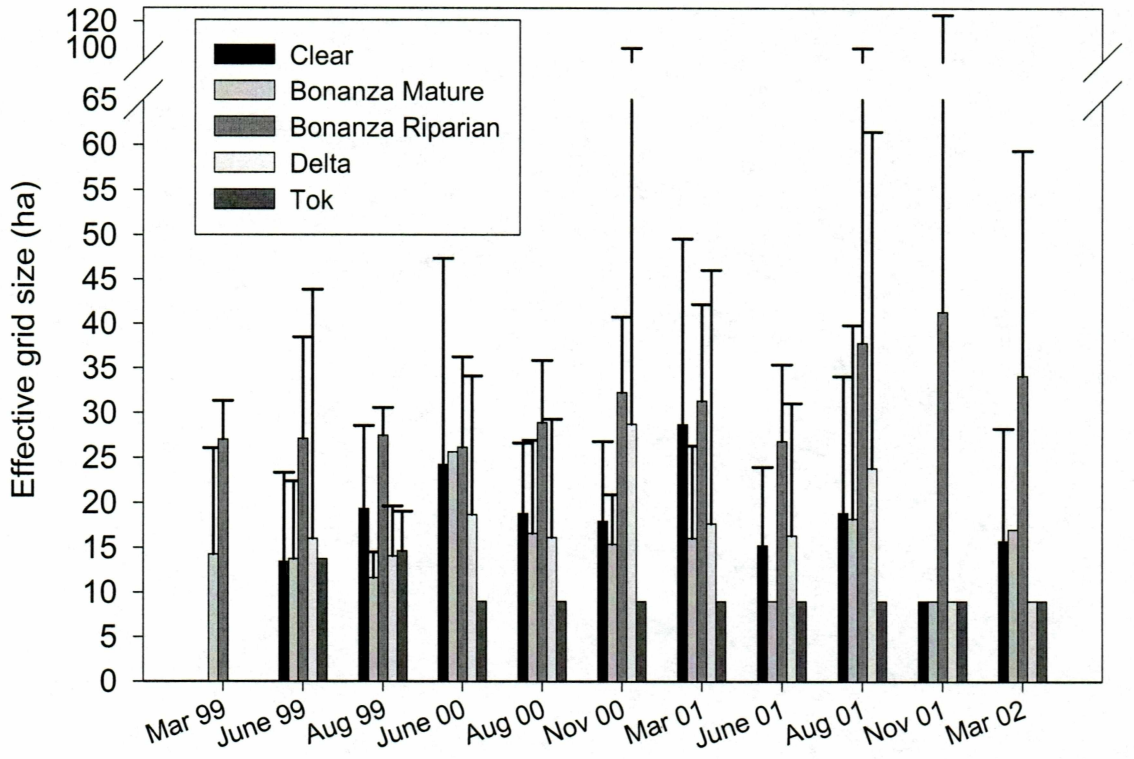

Figure 1.3. The effective trapping area (estimated from MMDM) of primary encounter occasions for the 5 trapping grids in Interior Alaska. Error bars represent 95% confidence intervals. Effective grid sizes without uncertainty estimates were calculated from number of hares captured (M_{t+1}) and/or did not have adequate recaptures for estimation of movement.

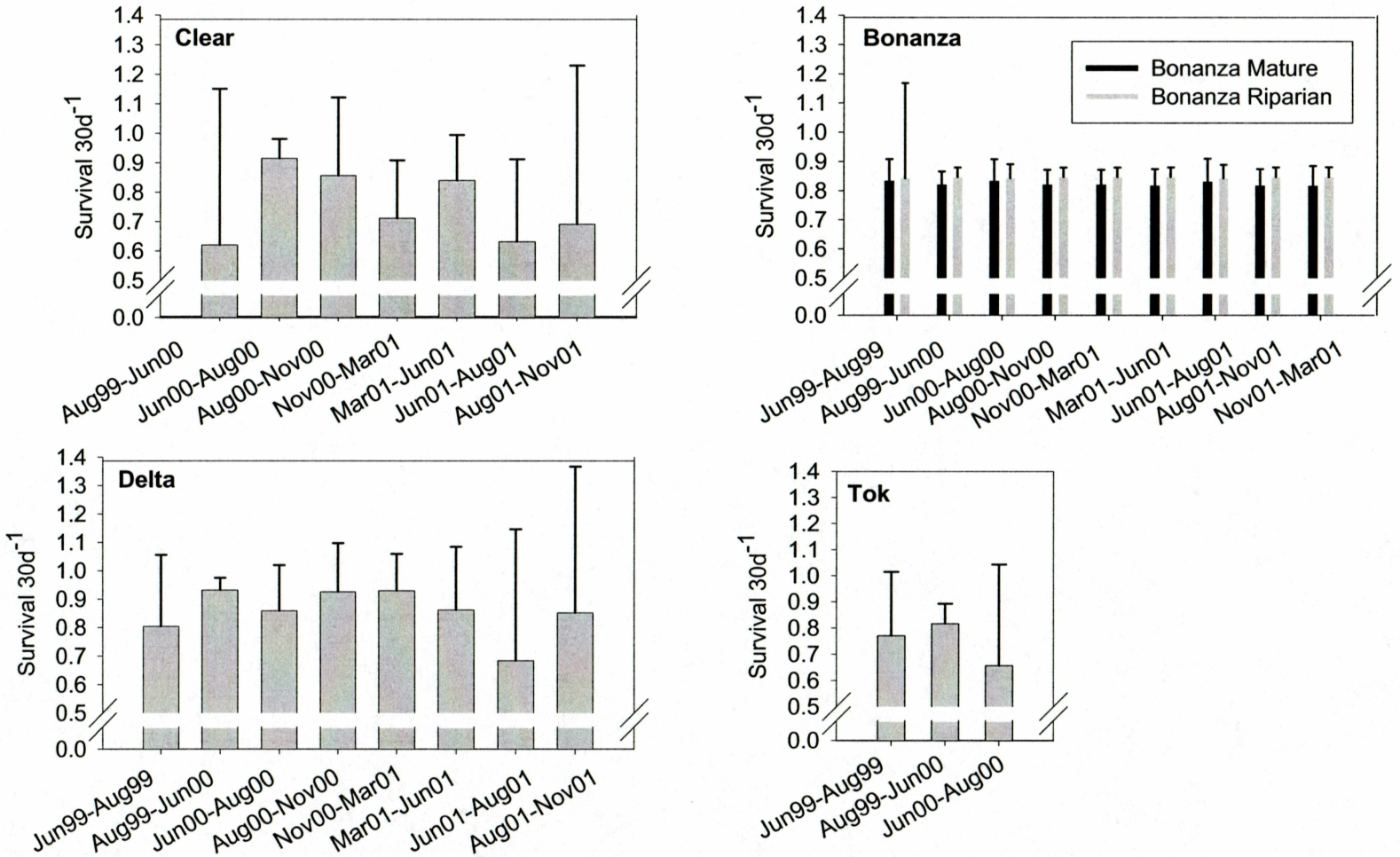

Figure 1.4. Adult survival (30-day) of snowshoe hares estimated at 5 trapping grids in Interior Alaska and corresponding 95% confidence intervals.

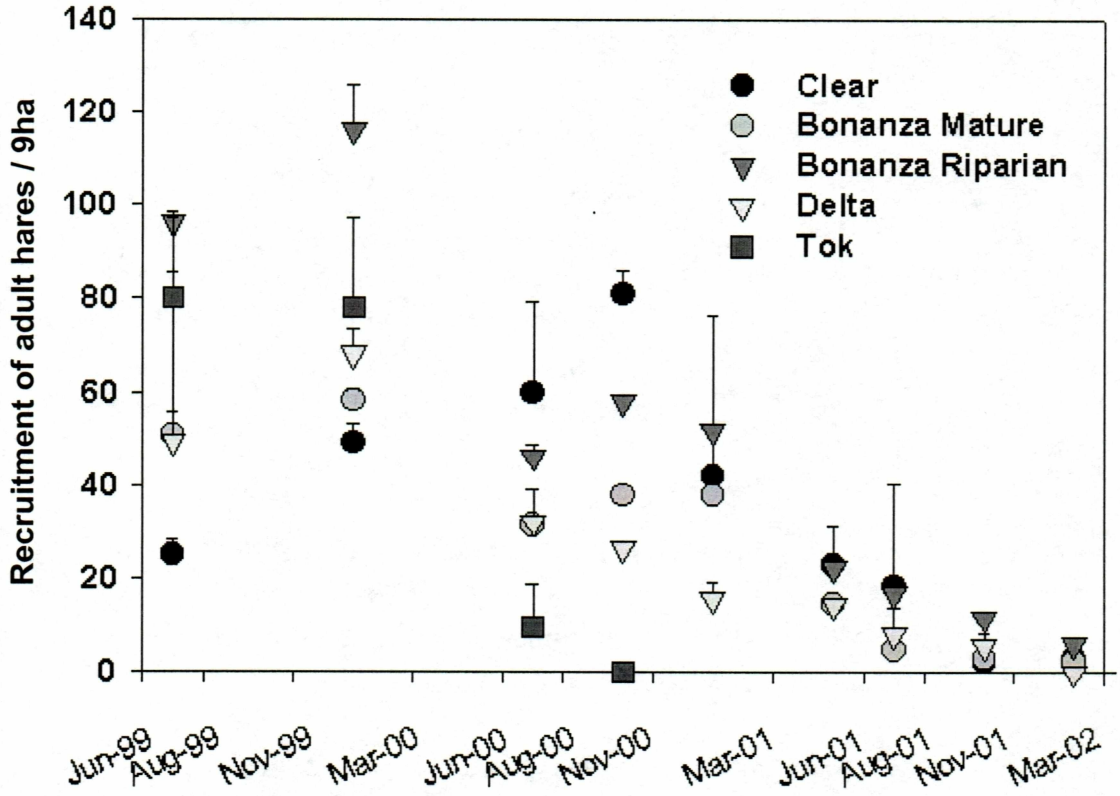

Figure 1.5. Adult recruitment (30-day) of snowshoe hares among primary encounters at the 5 trapping grids in Interior Alaska. Recruitment was estimated using Pollock et al. (1990:21).

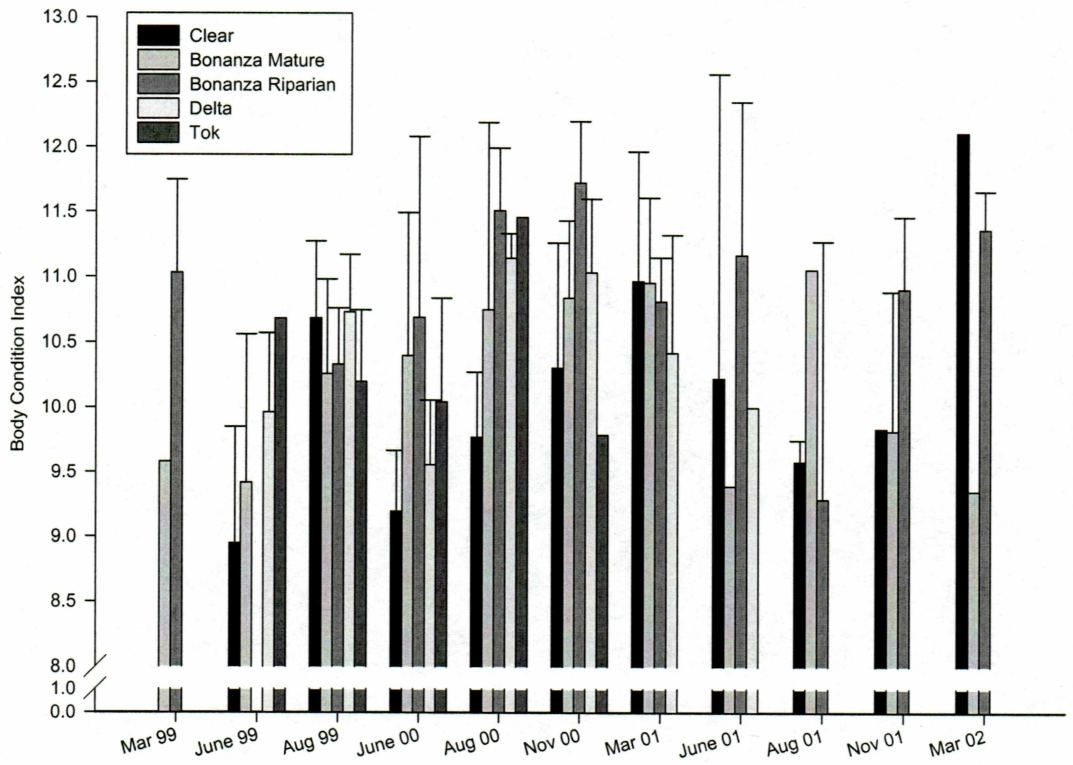

Figure 1.6. Indices of body condition of adult male snowshoe hares among primary encounter occasions at the 5 Interior Alaska trap grids. Body condition equals mass (g) / right hind foot (mm).

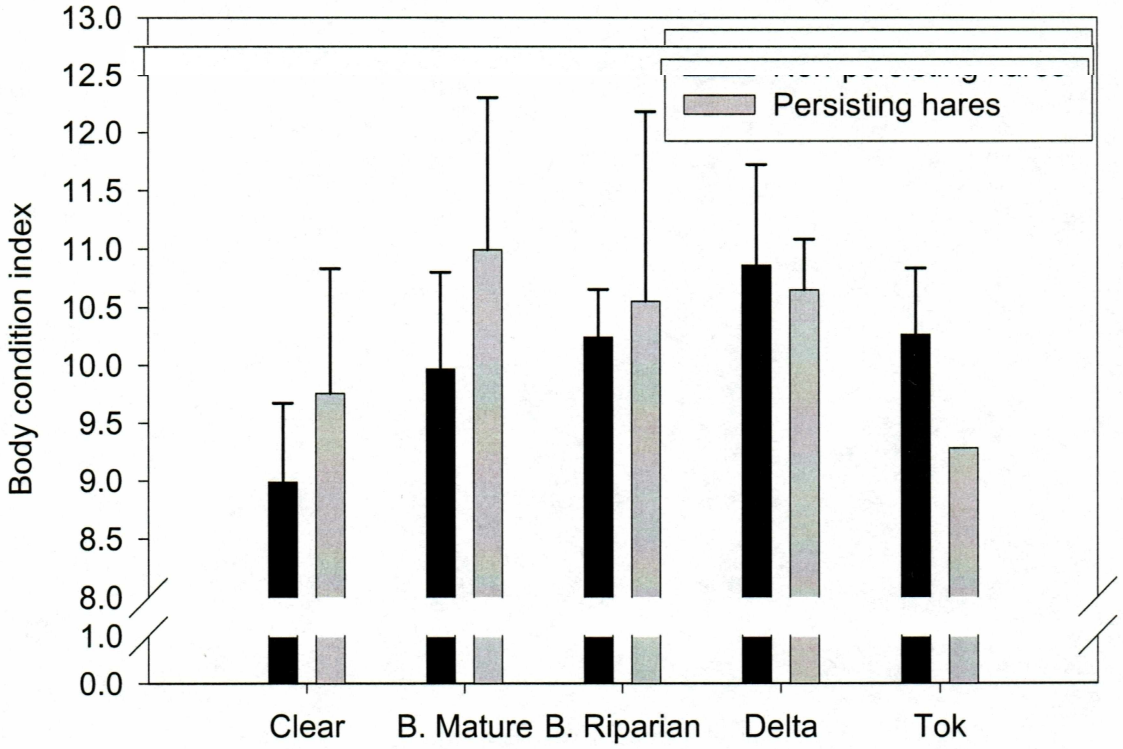

Figure 1.7. Indices of body condition of adult male snowshoe hares captured in August 1999 during high population densities at the 5 Interior Alaska trap grids. The 2 groups consisted of those later assumed dead and those that appeared following the population decline (post-August 1999).

Table 1.1. Program MARK model techniques of primary encounters using closed model type for *Lepus americanus*. Sites where male and female abundances were estimable are the sums of those abundance estimates. Inestimable male or female abundance initiated estimates derived without sex variation in capture recapture parameters.

Primary encounter	**Model groups**	**Model**
March 1999	B. Riparian B. Mature	M_{avg} M_{t+1}
June 1999	B. Mature and Riparian Clear, Delta and Tok	Sum of sexes M_{avg} M_{avg}
August 1999	All sites	Sum of sexes M_{avg}
June 2000	All sites	Sum of sexes M_{avg}
August 2000	All sites (excluding Tok) Tok	Sum of sexes M_{avg} M_{t+1}
November 2000	All sites (excluding Tok) Tok	Sum of sexes M_{avg} M_{t+1}
March 2001	All sites	M_{t+1}
June 2001	Clear All other sites	M_{avg} M_{t+1}
August 2001	All sites	M_{t+1}
November 2001	All sites	M_{t+1}
March 2002	All sites	M_{t+1}

Table 1.2. Model selection of primary encounters using closed model type. Variation in capture (p) and recapture (c) parameters included (p=c unless behavioral variation noted by ≠) null (.), temporal (t), diurnal (d), variation among first encounter session and remaining encounter sessions (1^{st}), heterogeneity (h), location (l), behavior (≠), sex (s), CAPT (T), exponential CAPT (T''), location variation among east and west sites (ew).

Primary encounter	Model groups	Model specification and AICc weights			
March 1999	M_{avg}	T = 0.3 null = 0.28	≠= 0.14 T'' = 0.13	1^{st} = 0.12 t = 0.04	
June 1999	Sum of sexes M_{avg} B. Mature males and B. Riparian females B. Mature females and B. Riparian males M_{avg}	null = 0.29 1st = 0.17 T = 0.15 d = 0.78 d = 0.43	≠= 0.1 s = 0.1 t = 0.13 d*ew = 0.349	d = 0.1 T*s = 0.05 t*s = 0.05 t = 0.213	d*s = 0.02 1^{st}*s = 0.02 d*l = 0.03
August 1999	Sum of sexes M_{avg} All sites	t*h = 1.00			
June 2000	Sum of sexes M_{avg} B. Mature and Tok Clear, B. Riparian, and Delta	null = 0.47 t = 0.42 t+d = 0.42	d = 0.21 d = 0.1 d*l = 0.06	l = 0.16. s(≠) = 0.01 s = 0.01	1^{st} = 0.16
August 2000	Sum of sexes M_{avg} All sites (excluding Tok)	d*s = 0.98	d*l = 0.01		
November 2000	Sum of sexes M_{avg} Delta B. Mature and B. Riparian: Clear:	null = 0.72 null = 0.42 T = 0.38 T = 0.25 1^{st} = 0.23 T*s =0.17	L(≠) = 0.01 l = 0.01 s*l = 0.01 s = 0.08 T'' = 0.08	1^{st} = 0.28 t = 0.069 null = 0.06	≠ = 0.04 s(≠) = 0.02
June 2001	M_{avg}	1^{st} = 0.28 d = 0.23	T = 0.21 null = 0.2	T'' = 0.08 t = 0.001	

Table 1.3. Model selection in Program MARK using robust design for variation in capture (p) and recapture (c) parameters of adult snowshoe hares. See Table 1.2 for descriptions of parameter variations.

	Model	**AICc weight**	**# parameters**	**Biological description**
Bonanza Mature and Riparian	p(d*S)=c(d*S)	1.00	42	Diurnal variation of secondary encounter occasions and seasonal variation of primary encounter occasions
Clear and Delta	p(d*m)=c(d*m)	1.00	33	Diurnal variation of secondary encounter occasions and variation of primary trapping months
Tok	p(d)=c(d)	0.883	7	Diurnal variation of secondary encounter occasions
	p(d*m)=c(d*m)	0.113	9	Diurnal variation of secondary encounter occasions and variation of primary trapping months
	p(d*t)=c(d*t)	0.004	13	Diurnal variation of secondary encounter occasions and temporal variation of primary encounter occasions

Table 1.4. Models were fit to data using robust design for variation in adult *L. americanus* survival parameters (Φ) for each modeling group. Variation included that described in Table 1.2 and year (y) and season (winter or summer) (S).

a) Bonanza

Model	**AICc (weight)**	**# parameters**	**Biological description**
Φ (l)	1137.88 (0.60)	15	Location variation of primary encounter occasions.
Φ (.)	1139.64 (0.25)	12	No variation of primary encounter occasions.
Φ (l*S)	1141.01 (0.13)	17	Location and seasonal variation of primary encounter occasions.
Φ (l*y)	1144.25 (0.02)	19	Annual and location variation of primary encounter occasions.
Φ (l*t)	1152.34 (<0.001)	29	Temporal and location variation of primary encounter occasions.

b) Clear and Delta

Model	**AICc (weight)**	**# parameters**	**Biological description**
Φ (l*t)	1079.62 (1.0)	33	Temporal and location variation of primary encounter occasions.
Φ (l)	1117.28 (0.0)	20	Location variation of primary encounter occasions.
Φ (l*S)	1127.20 (0.0)	22	Location and seasonal variation of primary encounter occasions.

c) Tok

Model	**AICc (weight)**	**# parameters**	**Biological description**
Φ (.)	170.38 (0.47)	5	No variation of primary encounter occasions
Φ (S)	171.45 (0.27)	6	Seasonal variation of primary encounter

CHAPTER 2. ASSESSMENT OF PELLET COUNTS AS RELIABLE PREDICTORS OF HARE DENSITY IN INTERIOR ALASKA[2]

Abstract

We counted fecal pellets deposited by snowshoe hares (*Lepus americanus*) in circular plots at 5 trap grids annually from 2000 to 2002 in Interior Alaska. Mean pellet counts were paired with estimates of hare density of the prior year for each trap grid. Annual hare densities were the mean densities of hares for each site from June, August, November, and March encounters. The resulting log-log regression between hare pellets and hare densities was weak (r=0.27, N=15). Density estimates of hares calculated from the functional regression describing the relationship of hare pellets and hare densities in Alaska contained large uncertainty despite being qualitatively similar to those from live trapping. Input of counts of hare pellets from Interior Alaska into a predictive log-log regression describing the relationship of hare pellets and hare densities in the Yukon Territory, Canada produced negatively biased estimates of hare densities when compared to those from live trapping. Estimation of hare densities using hare pellet counts should occur only if a significant relationship is found among hare pellets and hare densities in the area and/or habitat of interest. Intensive research that investigates temporal and spatial calibration of the hare pellet and

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[2] Flora, B.K., E.A. Rexstad, and K. Kielland. Submitted. Canadian Journal of Zoology.

hare density relationship and their collection methodology may decrease uncertainty associated with predicted estimates of hare density.

Introduction

Populations of snowshoe hares (*Lepus americanus*) experience 8-10-year fluctuations of density that affect boreal predator populations (Hodges 2000, O'Donoghue et al. 1997, Keith 1990), disrupt herbivore populations (Boonstra et al. 2001, Boutin et al. 1995), and influence associated vegetation and soil processes (Bryant 1987, Kielland et al. 1997, Kielland and Bryant 1998). Population monitoring of snowshoe hares, a 'keystone' species of the boreal forest, is difficult because current methods of estimating their populations such as mark-recapture are labor intensive and expensive (Krebs et al. 2001b, Murray et al. 2002). A factor that further limits intensive sampling of snowshoe hares is their relatively low economic value. The low economic value of an abundant species results in less labor and monetary resources devoted to their population sampling. Therefore, the implementation of density estimators that combine accuracy and efficiency are needed (Krebs et al. 2001b, Krebs et al. 1987). Predicting hare densities from the relationship of hare pellets and hare densities would increase wildlife biologists' ability to monitor snowshoe hare densities if the relationship is uniform across large-spatial scales (Krebs et al. 1987).

Regression of hare pellets and hare densities was described as a 'precise and efficient means of hare density measurement' in the Yukon Territory (Krebs

et al. 1987, 2001b). Previous to the Yukon Territory research, pellet counts have been described as proper indices of habitat use or population trends, but not valid for estimating population numbers (Wolff 1980). However, proponents have argued that monitoring of snowshoe hare density changes on an extensive spatial scale is possible with this simple technique because hares produce large numbers of pellets and drop them as they travel (Krebs et al. 1987, 2001b).

Krebs et al. (2001b) described the relationship of hare pellets and hare densities using a functional (Model II geometric means) regression (Ricker 1984, Sokal and Rohlf 1995, p. 541) of log-transformed hare pellet counts and hare densities given by:

$$\log_e\left(\text{population ha}^{-1}\right) = -1.203 + 0.889\log_e\left(\text{mean no. pellet}\right) \text{ (r=0.76, N=85).}$$

Krebs et al. (2001b) improved upon the linear relationship described in Krebs et al. (1987) (r=0.94) because the hare pellet: hare density relationship is curvilinear (Murray et al. 2002). Murray et al. (2002) showed that pellet counts are a robust estimator of hare numbers in low-density populations typical of their southern distribution. Similarly, Angerbjörn (1983) estimated a significant relationship among mountain hare (*Lepus timidus*) pellets and hare densities using linear regression of log-transformed data (r=0.95). However, the slope of the relationship between animal pellets and associated animal densities may vary geographically and temporally, and calibration is necessary for each locality and phase of the cycle (Krebs et al. 2001b). White (1992) argues that the efficiency

of pellet counts as density estimators is limited because validation of density indices can only occur with true density estimates.

Others describe the estimation of deer populations as accurate if pellet groups are recognizable (Bathceler 1975, Davis 1982). Limitations of estimating hare densities from hare pellets include changes of defecation rates due to diet changes or fluctuations in daily and seasonal activity patterns of hares (Hodges 1999). Furthermore, snowshoe hare pellets decay at different rates among habitat types despite some hare pellets persisting for over 20 years (Krebs et al. 2001a, Prugh, University of British Columbia, pers. comm.).

Our objective was to assess the relationship of hare pellets and hare densities at a landscape-scale in Interior Alaska. The relationships of hare pellets and hare densities were shown to be significant in the Yukon Territory (Krebs et al. 1987, 2001b) and northern Rocky Mountains (Murray et al. 2002). Our investigation provided insight into whether Krebs et al. (2001b) regressions could be applied northwest of the Yukon Territory *a priori* to testing or recalibration of the relationship of hare pellets and hare densities.

Methods

Snowshoe hare pellets were counted and hare densities estimated at 5 trap grids in Interior Alaska (Fig. 2.1). There were 2 trap grids at the Bonanza Experimental Forest 20 km south of Fairbanks (Bonanza Riparian = N64°41'36.6", W148°17'30.3 and Bonanza Mature = N64°41'41.7,

W148°17'03.4"), and 1 each near Clear Air Force Base (N64°17'23", W149°06'57.1"), mile1408 road on the Alaska Highway near Delta Junction (N63°54'50.2", W145°21'43.5"), and the Little Tok River at mile 97 of the Tok Cut-off Highway (N63°01'54.8", W143°22'14.5") (Fig. 2.1). The trap grids were 9 ha and consisted of 49-50 traps with inter-trap distances of 50 m (see **CHAPTER 1**). Snowshoe hare abundances for each site by primary encounter occasion were estimated using Program MARK (White et al. 1999), then transformed to hare densities using mean maximum distance moved (MMDM) (see **CHAPTER 1**). Using the terminology of Nichols and Pollock (1990), each population was monitored in 4 primary encounter occasions per year (June, August, November, and March). Annual hare densities were the mean of primary encounter occasions from June to March for each year of the study. Primary encounter occasions where there were no recaptures were declared M_{t+1} (the number of hares encountered), then divided by the 9 ha naïve trapping area and do not include an estimate of uncertainty. Additional site descriptions and hare density estimation methods applied were discussed in **CHAPTER 1**.

We counted hare pellets at 25 one-meter radius circles each located 3 m north of randomly selected traps. Pellet counts occurred during late spring trapping from 1999 to 2002, and the pellet plots were marked with wood stakes so that the same areas could be located the following year. Pellets were removed following the count as to avoid recounting pellets the following year. The pellet count circles differed from previously published research using counts

of hare pellets in that Krebs (1987, 2001b) applied long, thin quadrats (5.08X305 cm). Although means of pellet counts in small and large plots will have different predictive log-log regressions, the predicted density estimates should be similar as pellets are distributed randomly in the forest. Murray (2002) found that circular plots with 1 m radius were more likely to intercept hare pellets than rectangular plots in areas of low hare density, in that fewer circular plots than rectangular plots were devoid of hare pellets.

The hare pellets (independent) and hare densities (dependent) were assessed using techniques explained in Krebs et al. (1987, 2001b). Then, similar to Krebs et al. (2001b), the hare pellets (independent) and hare densities (dependent) were log-transformed because the variances increased with the means. The log-transformation does not alter the position of the major axis because scale units on the coordinate axes, and the configuration of points in the array, are independent of changes (log-transformation) in the measurement units used (Ricker 1984). Measurement error in both hare pellets (independent) and hare densities (dependent) further validated the assumptions of functional regression (Ricker 1973, 1984, Sokal and Rohlf 1995, p. 541).

The functional regressions calculated from populations in Interior Alaska and Krebs et al. (2001b) were employed to estimate hare densities from hare pellets collected in Interior Alaska. The functional regressions applied were:

$$\hat{D}_{\text{Yukon Territory hare estimate}} = \hat{\beta}_{\text{YukonTerritory}} + \hat{\beta}_{\text{YukonTerritory}} * (\text{Alaska pellets})$$

and

$$\hat{D}_{\text{Alaska hare estimate}} = \hat{\beta}_{\text{Alaska}} + \hat{\beta}_{\text{Alaska}} * (\text{Alaska pellets}).$$

Hare pellet counts from Interior Alaska were transformed to hare pellets per 0.16 m^2 prior to input into Krebs et al. (2001b) functional regression. The transformation was necessary due to the different dimensions of the plots used to count hare pellets in our study and that for the Yukon Territory. Hare densities estimated from the functional regressions were compared to hare densities estimated from live trapping using mean square error comparisons. Hare densities derived from the functional regressions were compared to hare densities from live trapping using a Spearman rank correlation. Mean square error combines both precision and bias when used to compare predicted and observed estimates.

Results

Populations of Snowshoe hares in Interior Alaska during the course of our study were at their highest densities in August 1999 and subsequently declined (Fig. 2.2, see **CHAPTER 1**). Mean counts of hare pellet were highest in 2000 and declined thereafter (Fig. 2.3). The annual means of snowshoe hare densities ranged from 5.32 (SE =0.99) to 0.166 (M_{t+1}) per hectare. Mean counts of hare pellets per circular plot ranged from 118.04 (SE=24.92) to 0.72 (SE =0.38) (Fig. 2.4).

The functional regression of snowshoe hare pellets and hare densities in Interior Alaska was:

$$\log_e(\text{population density ha}^{-1}) = -1.236 + 0.532\log_e(\text{mean no. pellets}).$$

The correlation coefficient of the above functional regression was 0.27, and the standard error of the slope was 0.14 (Fig. 2.4). The correction factor derived from Sprugel (1983) was 1.31. The correction factor was multiplied by hare densities estimated from the functional regression to lessen bias associated with natural log transformations (Krebs et al. 2001b, Sprugel 1983). Leverage coefficients describing the influence of the variates (Sokal and Rohlf, p. 531) ranged from 0.08 to 0.15 (Fig. 2.4).

Hare densities estimated from functional regressions describing the hare pellet to hare density relationships in Interior Alaska and the Yukon Territory (Krebs et al. 2001b) correlated similarly with those from live trapping ($r=0.814$, $P<0.001$, $N=15$). Densities estimated from the Interior Alaska functional regression were more similar than those of Krebs et al. (2001b) when compared qualitatively in sum of square comparisons (SS=23.35 and 50.94, respectively) (Fig. 2.5). However, Krebs et al. (2001b) estimates were more similar (MSE=52.71) than those from the functional regression for Interior Alaska (MSE=739.58) to observed estimates from live trapping when the associated errors were included (Fig. 2.5).

Discussion

The relationship among hare pellets and hare densities in Interior Alaska from 1999 to 2002 was weak. Further testing of the hare pellet: hare density relationship is required *a priori* to its application in hare population monitoring on a landscape-scale in Alaska. During the course of the study, snowshoe hare densities were highest in 1999 and declined thereafter. Densities of hares estimated from live trapping in Interior Alaska more closely resembled the estimates predicted from the functional regression derived from Interior Alaska than those produced from the functional regression for the Yukon Territory when uncertainty was excluded. The functional regression derived from hare populations in the Yukon Territory consistently resulted in hare densities that were negatively biased compared to those estimated from live trapping. However, estimates of hare density from the functional regression for Interior Alaska included 95% confidence intervals from 0-20 hares ha^{-1}. Snowshoe hare densities typically do not exceed 10 hares ha^{-1} (Krebs et al. 2001b). Therefore, further testing and re-calibration of the hare pellet: hare density relationship is required for Alaska.

Uncertainty associated with the hare pellet: hare density relationship would be minimized through intensive testing of methodology, such as dimensions of plots for counting pellets and number of pellet counts. Our methodology differed from that of Krebs et al. (2001b) in that we used circles rather than quadrats. Movement of snowshoe hares is not randomly distributed

through the forest, as hares select habitats for cover and commonly travel on runways (Hodges 1999, Hodges 2000, Wolff 1980). The long, thin 0.16 m^2 quadrats (Krebs et al. 1987, 2001b) may cross more hare runways than the circular plots; thereby, increasing pellet encounters. Furthermore, McKelvey et al. (2002) found that circular plots minimized bias associated with counting pellets on the plot boundary when compared to various rectangular pellet plots, including those dimensions applied by Krebs et al. (2001b). Hypothetically, increased pellet counts would shift the mean number of pellets (independent) of the regression to the right while hare densities (dependent) would remain the same. The slope of the functional regression would then decrease. However, the slope of the Interior Alaska functional regression was less (0.53) than that (0.89) of the functional regression for the Yukon Territory. The application of the Krebs et al. (2001b) pellet plot in our study would have further exaggerated the differences among the predicted hare densities derived from the functional regressions.

Another source of variation in the relationship of hare pellets and hare densities in Interior Alaska was the number of pellet counts employed. We employed 25 pellet counts using 3.14 m^2 pellet plots over 9 ha, whereas the Yukon Territory research employed 80 pellet counts using 0.16 m^2 pellet plots over 36 ha. The inter-trap distance and separation of transects in our study was 50 m, whereas the inter-trap distance in the Yukon Territory was 30 to 60 m and transects were separated by 120 m (Krebs et al. 2001b). Methodology applied in

our study and that of the Yukon Territory shows that we counted hare pellets in 8.72 m^2 per ha, whereas the research in the Yukon Territory sampled 0.34 m^2 per ha. The large difference in area sampled per ha among the studies highlights whether the area or number of points in the landscape estimated densities of hare pellets more accurately. The accuracy in estimating the relationship of hare pellets and hare densities may rely upon methodology employed in estimating densities of hare pellets. For instance, Murray (2002) encountered more pellets in 1 m^2 circular plots than rectangular plots used in Krebs et al. (2001b); however, each transect in Murray (2002) contained 10 m^2 of circular plots and 1.6 m^2 of rectangular plots. When the Murray (2002) pellet counts were transformed to pellet densities rather than mean number of pellets, the pellet densities were higher in the quadrats than the circular plots possibly due to reasons we have explained.

Snowshoe hare pellets are distributed non-randomly and clumped because hares travel on runways among areas of preferred habitat. The intensive testing of the relationship of hare pellets and hare densities should be preceded by analysis of different estimation techniques for pellet distributions and densities. Techniques for sampling pellet distributions and densities other than finding accurate pellet count plots should be addressed, such as those associated with distance sampling (Buckland et al. 1993). Distance sampling estimates object densities from line transects applying corrections to object distance from a selected transect (Buckland et al. 1993). The 3 assumptions of

distance sampling are that all objects on the line are detected, detected individuals are recorded at their original locations, and distances of objects from the line are measured without error (Thompson et al. 1998). This should be applicable to snowshoe hare pellets as they are readily detectable and do not move.

Indirect measures of snowshoe hare densities such as hare pellet counts may incorporate variation among habitat types, as hare pellets and hare densities may be affected by landscape heterogeneity. Landscape heterogeneity refers to variation in types and abundances of hare predators, and distributions of preferred food resources among habitat types. Snowshoe hare activity is influenced by availability of habitat coverage for predator avoidance, forage availability, breeding, and predation risk (Hodges 1999, Hodges 2000, Wolff 1980). Landscape heterogeneity associated with vegetation and soil may affect persistence of hare pellets. For instance, hare pellets degrade more quickly in spruce dominated habitat than under alders, and even more slowly beneath willows (Prugh, University of British Columbia, pers. comm.). Investigators should test whether heterogeneity associated with populations of plants and predator populations disrupts the distribution of snowshoe hare pellets prior to applying pellet counts across habitat types. Further disrupting the hare pellet: hare density relationship was that Murray (2002) showed that not all pellets persist for an entire year. Finding the differences in pellet persistence among habitat types would limit bias of pellet counts.

Finally, the methodology for estimating hare densities may affect the relationship of hare pellets and hare densities. Our population densities were dependent upon both movement and abundance (see **CHAPTER 1**). The movement adjustment may increase uncertainty, despite limiting the associated bias, of density estimates of hares. This was because 2 factors influenced uncertainty of density estimates rather than only uncertainty associated with population abundance. Furthermore, spatial calibration of the relationship of hare pellets and hare densities may require counts of hare pellets to occur simultaneously with estimation of hare densities. Simultaneously sampling both hare pellets and hare densities would limit uncertainty associated with averaging hare densities from primary encounter occasions that may be separated by 7 months, such as those from June to the following March. Sampling hare pellets during winter months may require an apparatus capable of sifting hare pellets from recent snowfall.

Proving that counting snowshoe hare pellets provides an accurate estimation of hare densities hinges on finding a significant relationship of hare pellets and hare densities in most landscapes (Krebs et al. 2001b). More intensive calibration than employed by our study is necessary if the methodology is to be used for snowshoe hare populations in Interior Alaska. Confirmation of the regressions may require further thought on pellet plot dimensions, number of plots per trap grid, and density estimation techniques for both hare pellets and hares. Therefore, estimating densities of snowshoe hares using indirect

measures such as pellet counts is not recommended as accurate methodology in Alaska.

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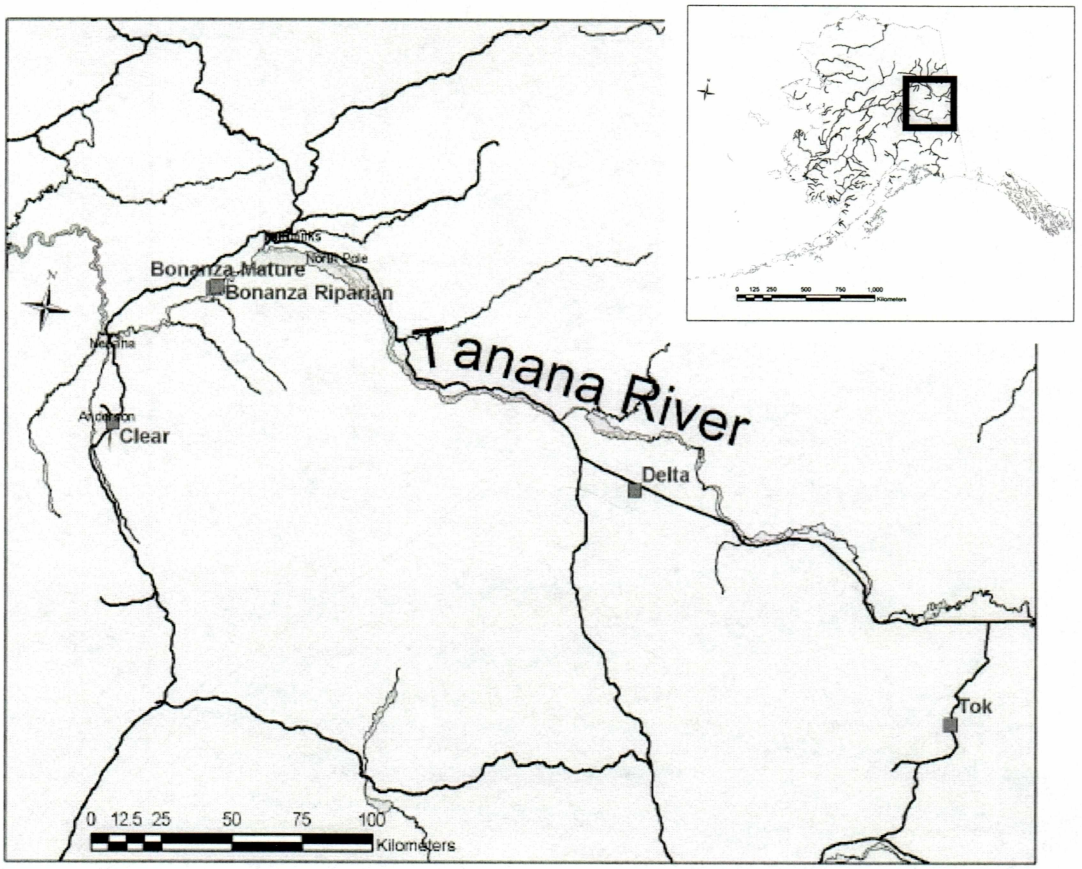

Figure 2.1. Location of the 5 trapping grids in Interior Alaska, USA where snowshoe hares were captured and hare pellets counted from 1999-2002.

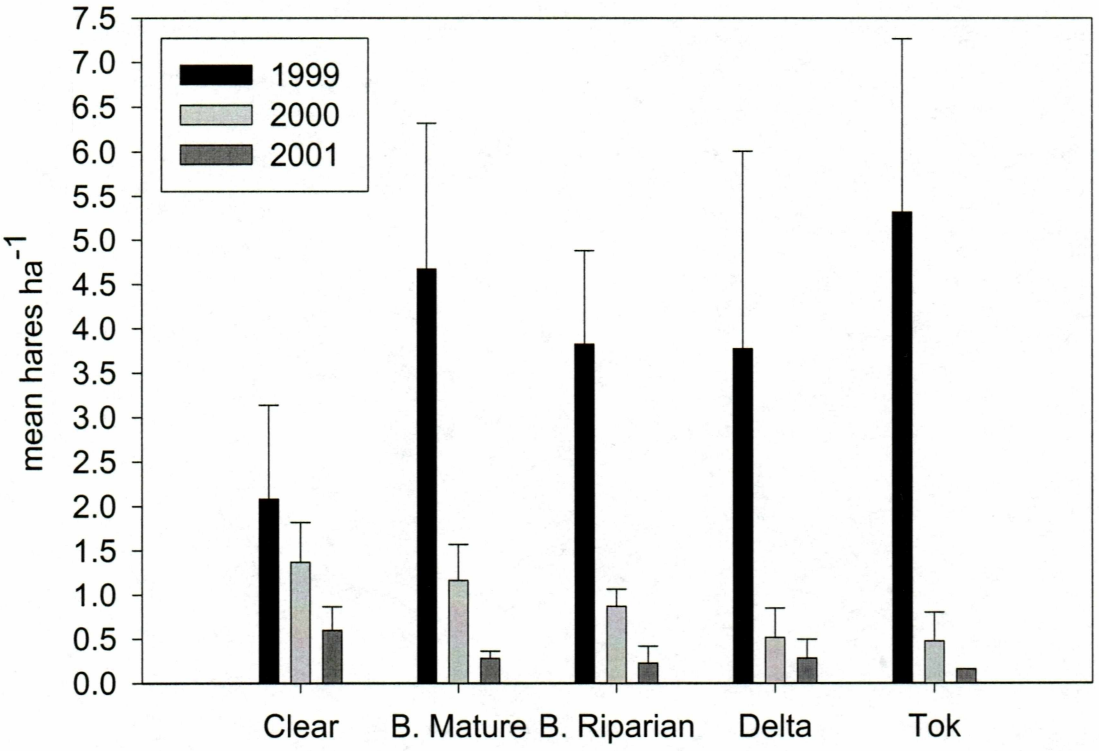

Figure 2.2. Annual mean densities of snowshoe hares from 5 trapping grids in Interior Alaska from 1999-2002. The error bars are the 95% confidence intervals.

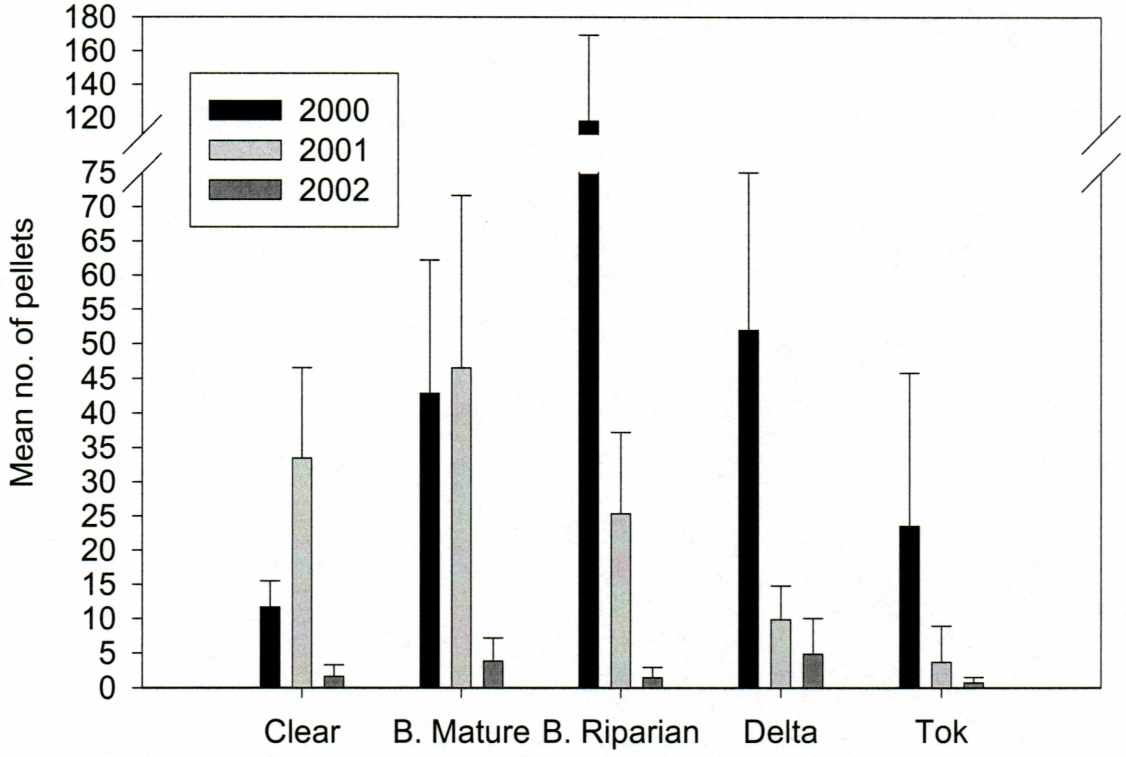

Figure 2.3. Mean counts of hare pellets from circular plots on 5 trapping grids in Interior Alaska from 2000-2002. The error bars are the 95% confidence intervals.

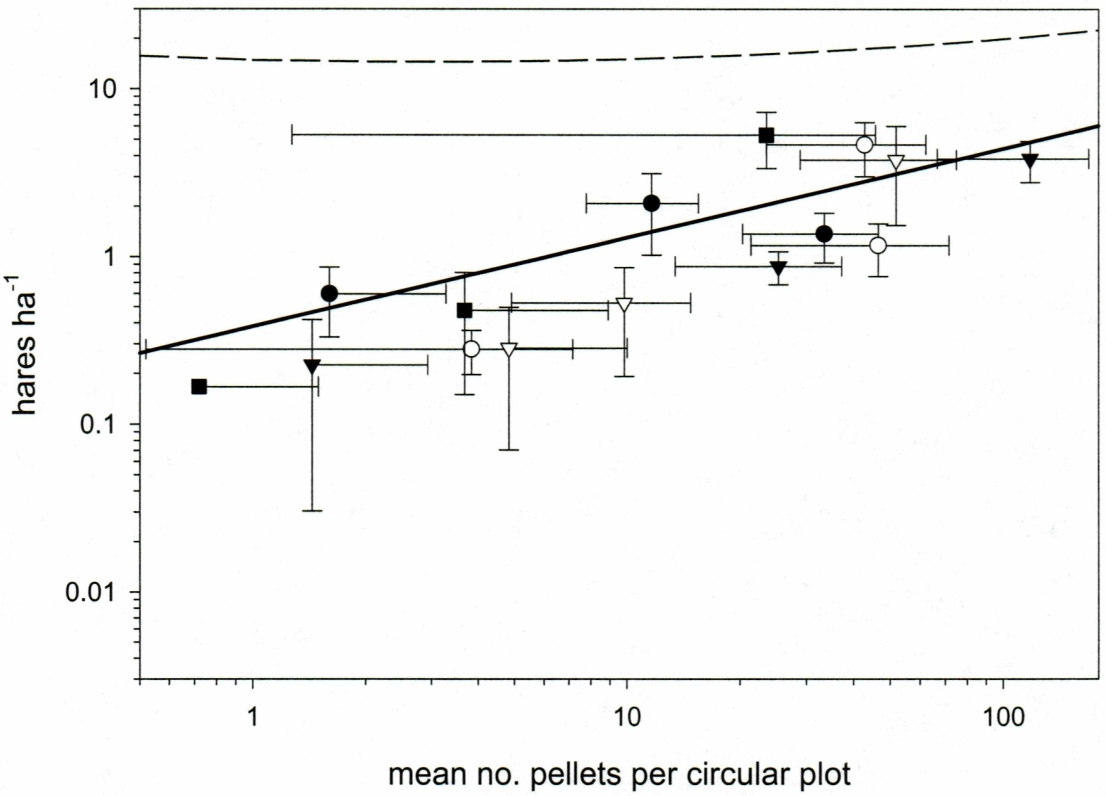

Figure 2.4. Mean number of hare pellets from circular plots (log scale) and annual mean densities of hares (log scale). The error bars are the 95% confidence intervals. The 3 years of data are shown for each trapping grid: Clear(•), Bonanza Mature (□), Bonanza Riparian (▼), Delta (▽) and Tok (□). The solid line is the functional regression estimated for the relationship of hare pellets and hare densities in Interior Alaska:

$$\log_e(\text{density ha}^{-1}) = 1.51 * \left[-1.236 + 0.532 \log_e(\text{mean no. pellets}) \right] \text{ (r=0.27, N=15).}$$

The dashed line is the upper 95% confidence limit of the functional regression.

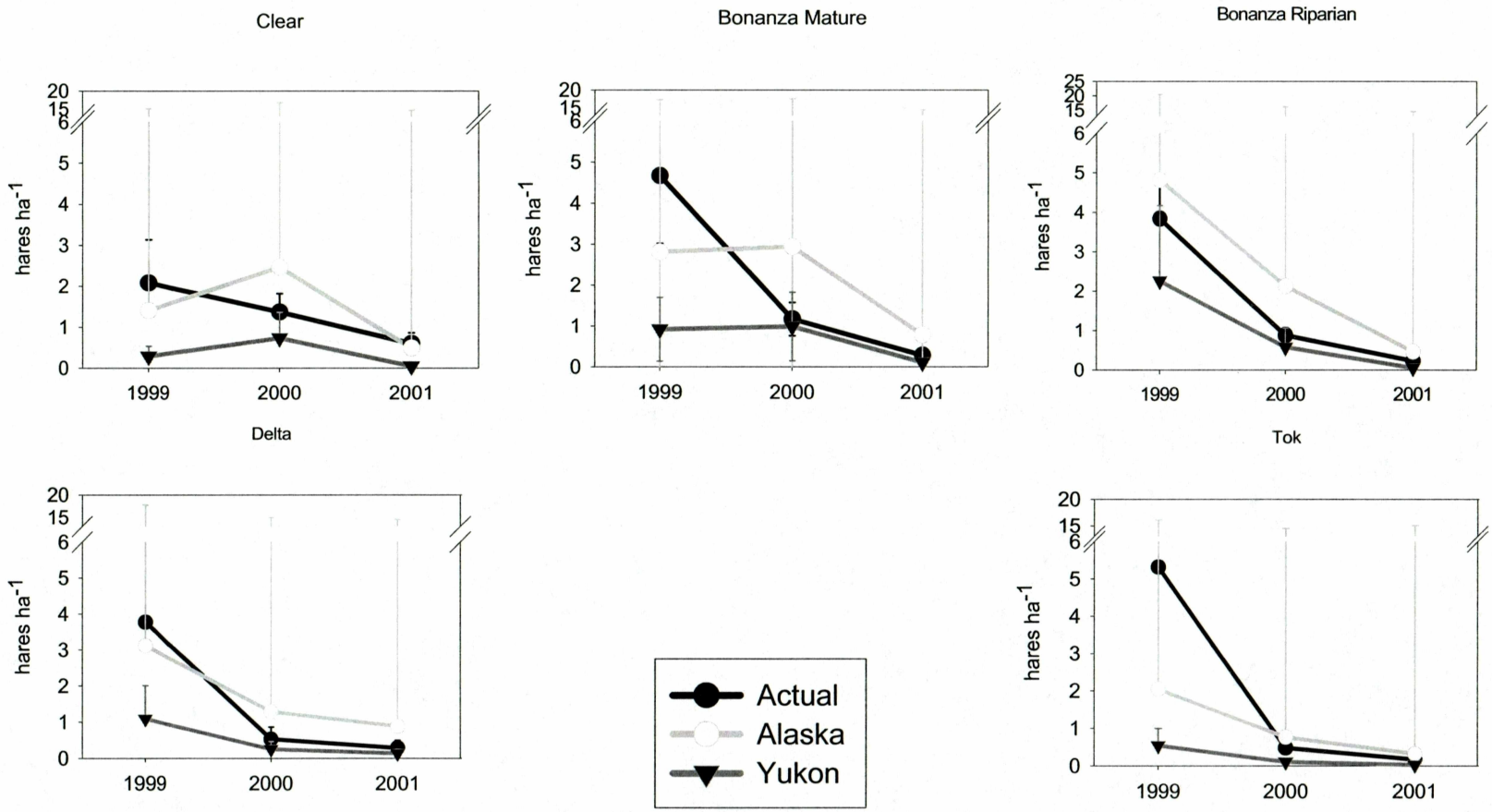

Figure 2.5. Comparison of hare estimates from live trapping to those estimated from hare pellets counted in Interior Alaska. Each of the 5 trapping grids are shown and the error bars represent the upper 95% confidence intervals.

CONCLUSION

Our description of population dynamics of snowshoe hares from peak to low in Interior Alaska adds a spatial component to previous hare research in Alaska (Ernest 1974, Wolff 1980, Trapp 1962). This study provides quantitative descriptions of an herbivore population for herbivore-plant research (Bryant 1987, Bryant et al. 1989, Kielland et al. 1997, Ruess et al. 1998) and predator monitoring by Alaska Dept. of Fish and Game (ADFG). Populations of snowshoe hares in Interior Alaska peaked in August 1999 and declined thereafter. Apparent survival varied temporally at 2 of the trap grids, whereas there was no variation in apparent survival at Bonanza, the site nearest Fairbanks. Population recruitment of adult hares was highest during high densities and declined to near zero within 3 years at all sites. The most rapid decline in densities, survival, and recruitment occurred in Tok immediately following the peak and none of the population attributes at the trap grid recovered by March 2002. Hares from the 1999 cohort that persisted through declining hare densities had qualitatively higher body conditions at three sites than those hares assumed to have died.

The densities of snowshoe hares at the peak differed qualitatively and variation in survival was dependent on locale. Additionally, the persistence effect related to body condition differed in magnitude spatially. Variation in population attributes among the 5 populations provides evidence that spatial comparisons of hare populations may be necessary prior to extrapolating conclusions from local-scale studies.

Another issue of concern was the temporal variation induced by the sampling design into our study. We attempted to assess the 4 locales in a short time by sampling the 5 trap grids in each primary encounter occasion in 5 weeks. In a perfect scenario, the hare populations would have been sampled simultaneously so that temporal variation in spatial comparisons would be eliminated. However, simultaneous trapping of all 5 trap grids was not possible as they were a large distance apart and the personnel required was not available.

Limiting temporal variation associated with sampling populations distributed on a landscape-scale may require more efficient techniques that retain accuracy of population estimates. However, biologists should limit use of indirect measures that incorporate uncertainty in dependent variables of predictive regressions if 'true density' is the objective. Because of the weak relationship among hare pellets and hare densities, estimating hare densities from hare pellet counts is currently unreliable in Alaska. If indirect measures are to be employed for predicting population densities, then *a priori* recalibration and intensive testing of the relationship among independent (hare pellets) and dependent (hare densities) variables is necessary. Recalibration and testing of the relationship should acknowledge specificity to spatial scale and habitats.

In detecting the proper scale for evaluating regional populations from local-scale conclusions, biologists should test whether heterogeneity in community dynamics, such as populations of plants and predators, affect hare

densities. Remember that the hare populations at our Tok trap grid declined rapidly following the high densities in 1999. A question stemming from our research is whether hare populations were more responsive to local or spatial scale differences in community dynamics of vertebrates and plants. Did differences in predator populations among our most distanced sites of Tok and Clear affect hare populations greater than differences in predator numbers in adjacent habitats at each of the sites? For instance, the magnitude of density fluctuations related to the hare cycle may differ depending upon size or number of refugia habitats available. Hare refugia have been described as having low predator numbers and high forage availability that allows hare numbers to recover from the low (Wolff 1980).

Once again, the quantitative description of Interior Alaska snowshoe hares from 1999 to 2002 provides herbivore data for ongoing studies of vegetation and soil processes (Long-Term Ecological Research Bonanza Creek Site) and associated predator populations (ADFG) in Alaska. Landscape heterogeneity may have influenced different levels of predator risk and forage availability for hares among the 5 trap grids. Further quantitative research of the interactions of hare populations and associated vertebrate and plant populations may describe the influence of landscape heterogeneity on populations of snowshoe hares in Alaska.

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